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THE COCHLEAR DUCT OF LIZARDS[1]

By

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Contents

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INTRODUCTION

The reptiles are not only the first vertebrates with a clearly defined cochlear duct, but also are remarkable in that they have experimented with the cochlear duct and have modified almost all its various parts. Among the reptiles we find differences in the overall size of the cochlear duct, in length, width, and configuration of the sound-sensitive cells constituting the papilla basilaris and marked alterations of the limbus, which is the supporting structure of the papilla basilaris. Differences are also noted in the enclosure of the perilymphatic fluid-filled spaces that transmit the sound-pressure waves to the medial aspect of the basilar membrane.

The avian cochlear duct is very similar to that found in the crocodiles. The mammalian duct is apparently also derived from a reptilian type, but is more specialized, elongated, and coiled.

The broad general features of the comparative anatomy of the membranous labyrinth of the vertebrate inner ear have been known for some time and have been most comprehensively presented by Retzius (1881, 1884) and more recently by de Burlet (1934). In 1953, Shute and Bellairs, in a study of the cochlear apparatus of certain gekkonid and pygopodid lizards, demonstrated that a detailed study of the cochlear duct had remarkable taxonomic implications. Recently, Hamilton (1960, 1964), Baird (1960a), and Schmidt (1964) have added much to the knowledge of the anatomy of the lizard inner ear and Wever and Vernon (1956, 1957, 1958, and 1960), Wever *et al.* (1963a, 1963b, and 1964), Wever and Peterson (1963), and Crowley (1964) have indicated something of the various functional capacities of the reptilian cochlea.

It is now obvious that detailed studies of the structure and function of reptilian cochleae will provide valuable information in the fields of bio-acoustics and reptilian taxonomy and phylogeny.

The recent studies of Hamilton and Baird (*op. cit.*) have helped clarify the general anatomical relationships of lizard inner ear structures and the associated anatomical terminology. These studies, as well as those of Schmidt (*op. cit.*), were done largely by the time-honored and necessarily basic method of making serial sections, and from these, reconstructions.

The present approach to the study of the reptilian inner ear is somewhat different in that, in addition to serial sections, the entire cochlear duct has been dissected out of the animal, and its anatomy studied by direct observation of the three-dimensional structure of the intact apparatus. That this is the same approach used by Retzius, in 1884, is apparent if one studies the illustrations of his great work. While he presented the general features of the anatomy of the membranous labyrinth in a variety of lizards (Iguanidae, Lacertidae, Gekkonidae, Chamaeleonidae, Anguidae, and Scincidae), he did not report the detailed anatomy of the cochlear duct in these animals. The object of this paper is to describe and illustrate the gross anatomical features of the cochlear duct of lizards.

Materials and Methods

Since histologic serial sections of the entire posterior cranium are most helpful in an anatomic study of the vertebrate inner ear, lizards from a number of families were sacrificed by decapitation, the heads fixed in a variety of ways, and after decalcification, embedded in paraffin or celloidin and serially sectioned.

After study and reconstruction of serial sections of various lizard inner ears, it became apparent that by careful dissection one could remove the cochlear duct intact from the otic capsule. Trials on freshly sacrificed lizards soon verified the simplicity and great utility of this procedure (see below).

Since the present study is not concerned with the histology of the cochlear duct, but is limited primarily to gross structures, details of histologic preparation will not be presented at this time.

While tissue from freshly sacrificed animals is necessary for histological preparations, museum specimens provide excellent material for the study of gross anatomical features of the otic capsule and its contained structures. Thus, intact cochlear ducts were removed from both live animals and a large variety of specimens in the herpetological collections of the California Academy of Sciences and of the Division of Systematic Biology of Stanford University.

It is possible to remove the cochlear duct from a reptile with only minimal damage to the specimen. A three-sided flap, involving little or no damage to head scales, over the otic area of the left side of the head was folded downward exposing the posterolateral aspect of the cranium. Overlying muscle or extensions from roofing bones were carefully dissected away exposing the lateral aspect of of the otic capsule. The tip of a scalpel or a dental drill was then employed to open the otic capsule exposing the sacculus and cochlear duct. The sacculus was usually removed and the auditory nerve transected at its point of emergence through the medial wall of the capsule; then the cut distal end of the nerve was grasped with fine forceps and the cochlear duct lifted free from the cochlear recess.

In the great majority of museum specimens, the original preserving alcohol or formalin had penetrated the otic capsule in time to preserve even the cellular elements of the papilla basilaris. In large thick-boned specimens such as *Sphenodon, Heloderma,* and *Amblyrhynchus*, some details were indistinct because the preserving agent could not penetrate the capsule fast enough to completely inhibit autolysis.

After removal of the intact cochlear duct, it was stored in 70 per cent ethyl alcohol for further study. The structural details of the cochlear duct were more easily seen if the calcium carbonate crystals were removed from the otolithic membrane overlying the macula lagenae. This was easily accomplished by soaking the specimen overnight in a vinegar–alcohol solution.

Visualization of the details of the papilla basilaris and its supporting limbus required removal of the lateral wall (vestibular membrane) of the cochlear duct with fine forceps and scissors.

All cochlear ducts were photographed in stereocolor and black and white, and scale drawings were made of each specimen. After characteristic family types were established, a professional artist, Mr. Wayne Emery, executed drawings of both the lateral and medial aspects of the cochlea using the actual specimens.

For the present study the following measurements were made of each cochlear duct: the greatest length and width of the entire duct and the limbus, and the lengths of the papilla basilaris and macula lagenae. Measurements were made by means of a calibrated reticule placed in the eyepiece of a dissecting microscope.

The length of the papilla basilaris was estimated to the nearest 0.05 mm. and the approximate area determined by tracing the outline of the papilla basilaris on an appropriately ruled paper, and the areal value determined by use of a Leitz planimeter. While the length of the papilla basilaris was determined for all species studied, the area was calculated for a little less than half the number (see table 2).

Since the macula lagenae is usually curved, its length could only be very generally estimated. The area was not determined in the present study, for this would have required dissection and consequent destruction of the specimens.

In most cases the measurements reported in the tables and graphs are based on one specimen only. That measurements from a single specimen do provide useful data was verified by measuring series of adult specimens of *Cnemidophorus tigris* (25), *Xantusia vigilis* (20), *Mabuya multifasciata* (6), *Gerrhonotus multicarinatus* (6), and *Dipsosaurus dorsalis* (6). In this sampling, no feature of the cochlear duct varied in its measurements more than 15 per cent within one species.

In 25 adults of *Cnemidophorus tigris* varying in snout–vent length from 73 to 105 mm., the cochlear duct length varied from 1.7 to 2.0 mm. (15% variation) and the limbus from 1.2 to 1.4 mm. (14%). There was no correlation between these measurements and snout vent length of adult animals. The length of the papilla basilaris was very close to 0.8 mm. in all 25 specimens.

To determine the effect of growth on cochlear duct elements within a single species, seven specimens of *Leiolopisma assatum*, ranging from very young (27 mm. snout–vent length) to fully mature animals (53 mm. snout–vent length) were studied. Graph 1 (p. 276) demonstrates that the cochlear duct increases approximately 10 per cent in length and the limbus, 15 per cent, but that the papilla basilaris remains essentially the same length during the postnatal growth of a species. To show the relationship between body size and the length of the cochlear duct and the papilla basilaris in those families where sufficient data were available, such information is presented in graph form (graphs 2–7). While most animals used were adult, if a specimen were immature the dimensions of the cochlear duct and its elements might seem out of proportion to other members of the family. In those families that have but few representatives or where the available material is limited, the above data are presented in table 2 (p. 272).

The present study is based on a gross anatomical examination of the cochlear ducts of 205 species of lizards representing 131 genera and 18 families. Representatives of all living lizard families except the Anelytropsidae, Shinosauridae, and Lanthanotidae were studied.

In addition to the lizards, samples of several families of snakes and turtles have been studied and for purposes of comparison, the cochlear duct of a turtle, a snake, and *Sphenodon* are described and illustrated.

Table 1 is a list of material examined.

Observations

A. General Anatomical Features.

The recent excellent studies of Hamilton (1960, 1964) and Baird (1960a) have greatly clarified the general anatomy of the membranous labyrinth of lizards. For ease of understanding general anatomical relationships, schematic representations of the lateral and inferior aspects of the skull and drawings of the entire membranous labyrinth (lateral and medial views) of *Xantusia vigilis* are presented (figs. 1–4).

The cochlear duct (figs. 3 and 4) is the most inferior portion of the membranous labyrinth and is connected with the sacculus by the sacculo-cochlear

Table 1. *List of materials examined.*

LACERTILIA	
Iguanidae	
Amblyrhynchus cristatus	(CAS 87102 [59])[1]
Anolis antiquae	(SU 7473 [154])[2]
Anolis biporcatus	(CAS 67165 [65])
Anolis carolinensis	(CAS 63340 [66])
Anolis copei	(CAS 79146 [58])
Anolis cristatellis	(SU 18702 [146])
Anolis equestris	(SU 14608 [232])
Anolis cupreus	(CAS 87836 [132])
Anolis distichus	(SU 14571 [151])
Anolis polylepis	(CAS 79287 [77])
Anolis sallaei	(CAS 68086 [93])
Basiliscus vittatus	(CAS 23)[3]
Brachylophus fasciatus	(CAS 50135 [133])
Callisaurus draconoides	(CAS [16])
Chalaradon madagascariensis	(CAS 54659 [115])
Corythophanes hernandezi	(SU 18344 [193])
Crotaphytus collaris	(CAS [18])
Crotaphytus wislizeni	(No data, CAS [14])
Ctenosaurus pectinata	(CAS [161])
Ctenosaurus similis	(CAS 69291 [171])
Dipsosaurus dorsalis	(CAS [163], + 6 specimens)
Holbrookia texana	(CAS 31260 [39])
Hoplocercus spinosus	(CAS 93805 [70])
Iguana iguana	(CAS [162], + 3 specimens)
Leiocephalus carinatus	(SU 14611 [159])
Liolaemus pictus	(CAS 85249 [99])
Mariguana agassizi	(CAS 62604 [90])
Norops auratus	(CAS 79376 [98])
Oplurus cuvieri	(SU 13950 [191])
Petrosaurus thalassina	(CAS 90946 [96])
Phrynosoma coronatum	(CAS 40170 [56])
Phrynosoma douglassi	(CAS 48854 [204])
Phrynosoma m'calli	(CAS 33657 [222])
Phrynosoma modestum	(CAS 13110 [216])
Phrynosoma platyrhinos	(CAS 65315 [210])
Plica plica	(CAS 14550 [94])
Sauromalus obesus	(CAS [35], + 3 specimens)
Sceloporus magister	(CAS [15 and 19])
Sceloporus occidentalis	(CAS [288], + 4 specimens)
Tropidurus albemarlensis	(CAS 11435 [95])

[1] The first number is the California Academy of Sciences, Department of Herpetology catalogue number of the specimen. The number in brackets is the catalogue number of the cochlear duct which is preserved separately in the collections of the Department of Herpetology of the Academy.

[2] Stanford University, Division of Systematic Biology catalogue number.

[3] Uncatalogued fresh specimen, cochlear duct only preserved.

Table 1. Continued.

Tropidurus hispidus	(CAS 49413 [102])
Tropidurus peruvianus	(CAS 80905 [103])
Tropidurus semitaeniatus	(CAS 49455 [221])
Tropidurus torquatus	(SU 9450 [236])
Uma scoparia	(CAS 42119 [97])
Urosaurus ornatus	(CAS 35069 [218])
Urostrophus torquatus	(CAS 85236 [181])
Uta stansburiana	(CAS [17])
Xiphocercus valensiennesii	(SU 9307 [199])
Agamidae	
Agama agilis	(CAS 86343 [25])
Agama nupta	(CAS 86509 [165])
Agama persica	(CAS 86522 [202])
Amphibolurus barbatus	(CAS 77569 [160])
Amphibolurus muricatus	(CAS 77618 [172])
Calotes versicolor	(CAS 16880 [219])
Chlamydosaurus kingii	(CAS 77537 [72])
Draco rizali	(CAS 60368 [30])
Gonyocephalus grandis	(CAS [194, 195])
Gonyocephalus modestus	(SU 13555 [150])
Hydrosaurus pustulosus	(CAS 62381 [169])
Japalura polygonata	(CAS 21309 [170])
Japalura swinhonis	(CAS 18088 [174])
Phrynocephalus nejdensis	(CAS 84375 [144])
Sitana ponticeriana	(CAS 94355 [211])
Tympanocryptis lineata	(CAS 77624 [209])
Uromastix loricatus	(CAS 86463 [166])
Chamaeleonidae	
Brookesia superciliaris	(CAS 55118 [43])
Chamaeleo bitaeniatus	(CAS 85766 [42])
Chamaeleo brevicornia	(CAS 54681 [50])
Chamaeleo dilepis	(No data, CAS [9])
Anguidae	
Anguis fragilis	(CAS 66314 [88])
Diploglossus lessonae	(CAS 49540 [61])
Gerrhonotus coeruleus	(CAS 39105 [186])
Gerrhonotus multicarinatus	(CAS [20, 286], + 6 specimens)
Ophisaurus ventralis	(CAS 49063 [60])
Anniellidae	
Anniella pulchra	(CAS 39198 [44, 45], + 4 specimens)
Xenosauridae	
Xenosaurus grandis	(CAS 87839 [344])
Helodermatidae	
Heloderma suspectum	(CAS [6])
Heloderma horridum	(CAS 53929 [201])

Table 1. Continued.

Varanidae	
Varanus nuchalis	(CAS 15766 [141])
Varanus punctatus	(CAS 77677 [84])
Varanus salvator	(CAS 61120 [114])
Varanus species	(CAS [284])
Lacertidae	
Acanthodactylus cantoris	(CAS 86555 [180])
Eremias argus	(CAS 86904 [188])
Eremias guttulata	(CAS 91601 [51])
Eremias guttulata	(CAS 91599 [52])
Lacerta dugesi	(CAS 94081 [3])
Lacerta dugesi	(CAS 94072 [4])
Lacerta viridis	(CAS [105])
Lacerta viridis	(SU 22995 [106])
Lacerta vivipara	(SU 18472 [104])
Psammodromus algirus	(CAS 92431 [53])
Psammodromus hispanicus	(SU 17279 [235])
Takydromus septentrionalis	(CAS 66112 [46])
Teiidae	
Anadia bogotensis	(SU 8282 [229])
Ameiva ameiva	(CAS 7063 [33])
Ameiva aquilini	(CAS 39431 [49])
Ameiva undulata	(CAS 68884 [41])
Bachia peruana	(CAS 93231 [182])
Dicrodon lentiginosus	(CAS 94737 [152])
Cnemidophorus communis	(CAS 58803 [189])
Cnemidophorus gularis	(CAS 34537 [179])
Cnemidophorus hyperthrus	(CAS 8634 [168])
Cnemidophorus maximus	(CAS 46207 [187])
Cnemidophorus melanosthethus	(CAS 39105 [190])
Cnemidophorus ocellatus	(CAS 49555 [178])
Cnemidophorus tigris	(CAS 88334 [1])
Cnemidophorus tigris	(CAS [12, 13, 282])
Cnemidophorus tigris	(CAS [315–340])
Kentropyx calcaratus	(SU 8330 [113])
Neusticurus ecpleopus	(SU 8370 [158])
Pantodactylus species	(SU 17287 [230])
Proctoporus unicolor	(SU 15813 [234])
Tupinambis teguixin	(CAS 89669 [100])
GEKKOTA	
Eublepharidae	
Coleonyx species	(CAS 5637 [10])
Coleonyx variegatus	(CAS [304, 305])
Eublepharus species	(CAS 86383 [127])
Gekkonidae	
Aristelliger nelsoni	(CAS 39418 [134])
Bavayia sauvagii	(CAS 80835 [116])

Table 1. Continued.

Cosymbotus platyurus	(SU 18566 [148])
Cyrtodactylus annulatus	(CAS 60207 [121])
Cyrtodactylus scaber	(CAS 84532 [118])
Gecko gecko	(CAS [300, 301])
Gecko japonica	(CAS 21749 [139])
Gehyra mutilata	(SU 9149 [156])
Gehyra oceanica	(SU 21778 [157])
Gehyra variegatus	(CAS 76237 [47])
Gehyra variegatus	(CAS 76248 [48])
Hemidactylus frenatus	(SU 9545 [147])
Hemidactylus garnotii	(CAS 47411 [131])
Hemidactylus persicus	(CAS 86454 [128])
Hemidactylus turcicus	(CAS 87114 [354])
Heteronata binoei	(CAS 74805 [126])
Hoplodactylus granulatus	(CAS 47982 [120])
Lepidodactylus lugubris	(SU 9389 [155])
Microgecko helenae	(CAS 93936 [122])
Oedura marmorata	(CAS 75234 [125])
Oedura robusta	(CAS 75671 [137])
Pachydactylus maculatus	(CAS 85889 [109])
Phelsuma madagascariensis	(CAS [302, 304])
Phyllodactylus bauri	(CAS 9745 [124])
Phyllodactylus elisae	(CAS 86352 [110])
Phyllodactylus marmoratus	(CAS 83590 [107])
Phyllodactylus muralis	(CAS 73567 [130])
Phyllodactylus unctus	(CAS 91356 [108])
Phyllurus cornutus	(CAS 44119 [117])
Stenodactylus sthenodactylus	(CAS 84210 [112])
Teratoscincus scincus	(CAS 84648 [119])
Thecadactylus rapicauda	(SU 8335 [73])
Tarentola mauritanica	(SU 18114 [145])
Sphaerodactylidae	
Gonatodes fuscus	(CAS 71228 [111])
Sphaerodactylus argus	(SU 14991 [149])
Sphaerodactylus cinereus	(CAS 39290 [64])
Uroplatidae	
Uroplatus fimbriatus	(SU 13473 [231])
Pygopodidae	
Aprasia pulchella	(SU 16223 [198])
Lialis burtonis	(CAS 77655 [34])
Pygopus lepidopodus	(CAS 77659 [206])
Scincidae	
Ablepharus lineocellatus	(CAS 83798 [81])
Acontias meleagris	(CAS 84188 [225])
Aulacoplax leptosoma	(SU 20822 [228])
Brachymeles gracilis	(CAS 92855 [82])
Brachymeles schadenbergi	(CAS 60493 [205])
Brachymeles tridactylus	(SU 19426 [123])

Table 1. Continued.

Brachymeles vermis	(CAS 60721 [220])
Chalcides polylepis	(CAS 92389 [215])
Chalcides sepoides	(CAS [36])
Dasia smaragdinum	(CAS 60500 [69])
Egernia nitida	(CAS 76612 [76])
Egernia striolata	(CAS 83931 [101])
Emoia nigra	(CAS 72238 [142])
Eumeces elegans	(CAS 31899 [38])
Eumeces fasciatus	(CAS 71565 [173])
Eumeces gilberti	(CAS 89417 [75])
Eumeces obsoletus	(CAS 71599 [55])
Eumeces stimsonii	(CAS 21670 [37])
Hemisphaeriodon gerrardi	(CAS 76692 [135])[1]
Leiolopisma assatum	(CAS 68571 [80])
Leiolopisma assatum	(CAS [347–353])
Leiolopisma guichinoti	(CAS 83856 [79])
Leiolopisma noctua	(CAS 64036 [54])
Lygosoma laterale	(CAS 17997 [78])
Lygosoma lentiginosus	(CAS 83737 [214])
Lygosoma verrauxi	(CAS 83738 [212])
Mabuya mabouia	(CAS 71454 [89])
Mabuya multicarinata	(CAS 60435 [74])
Mabuya multifasciata	(CAS 85672 [68])
Mabuya multifasciata	(CAS [299], + 6 specimens)
Nessia monodactyla	(CAS 17164 [207])
Ophiomorus tridactylus	(CAS 84674 [143])
Otosaurus cumingi	(SU 19591 [192])
Rhodona fragilis	(CAS 77196 [67])
Riopa bowringii	(CAS 75671 [136])
Scincus philbyi	(CAS 84585 [85])
Sphenomorphus indicus	(CAS 18685 [86])
Sphenomorphus quoyi	(CAS 76869 [91])
Sphenomorphus variegatus	(CAS 60281 [184])
Tiliqua scincoides	(CAS no number [7, 8])
Trachysaurus rugosus	(CAS 76678 [71])
Tribolonotus gracilis	(SU 13659 [233])
Tropidophorus rivularis	(CAS 62005 [87])
Typhlosaurus cregoi	(CAS 85832 [92])
Feyliniidae	
Feylinia currori	(CAS 55111 [183])
Xantusiidae	
Klauberina riversiana	(CAS 43856 [27])
Klauberina riversiana	(CAS 43848 [28])
Lepidophyma flavomaculatum	(CAS 66489 [63])
Xantusia henshawi	(CAS 64632 [62])
Xantusia vigilis	(CAS [21, 22], + 6 specimens)

[1] It was discovered too late to be incorporated into the body of this paper that the nominal genus *Hemisphaeriodon* has been referred to the synonymy of the genus *Tiliqua*.

Table 1. Continued.

Cordylidae	
Cordylus cordylus	(SU 12086 [158])
Cordylus jonesii	(CAS [290])
Cordylus polyzonus	(CAS 84191 [29])
Gerrhosaurus flavigularis	(CAS [51])
Dibamidae	
Dibamus argenteus	(SU 18762 [83])
Amphisbaenidae	
Amphisbaena fuliginosa	(CAS 71336 [227])
Bipes biporus	(CAS 53726 [224])
Blanus cinereus	(CAS 92400 [226])
Diplometopon zarudnyi	(CAS 84534 [140])
Rhineura floridana	(CAS 14100 [213])
OPHIDIA	
Colubridae	
Pituophis catenifer	(CAS [291])
CHELONIA	
Testudinidae	
Gopherus berlandieri	(CAS [H46])
CROCODILIA	
Alligatoridae	
Alligator mississippiensis	(CAS [164], + 5 specimens)
RHYNCHOCEPHALIA	
Sphenodontidae	
Sphenodon punctatum	(CAS [40])

duct. The latter usually arises from the posteroinferior aspect of the sacculus, but may be more inferomedial in location in some families (Hamilton, 1964).

The cochlear duct in reptiles as exemplified in *Crotaphytus wislizeni* (figs. 5 and 6) characteristically contains two sensory areas. The macula lagenae usually occupies the anterior and anteroinferior portion of the duct, but frequently extends both anterolaterally and anteromedially. The macula lagenae is always covered by an otolithic membrane.

The papilla basilaris is a sensory area usually occupying a position on the medial wall of the cochlear duct and is usually associated with an overlying tectorial membrane. (Outline sketches showing the lateral and medial aspects of the cochlear duct of *Crotaphytus* are presented in figures 5 and 6; figures 7 and 8 are cross sections of the cochlear ducts of *Hemidactylus* and *Sauromalus*.)

The vestibular membrane makes up the lateral wall of the cochlear duct. The medial wall is more complex and in good part is formed of a modified connective

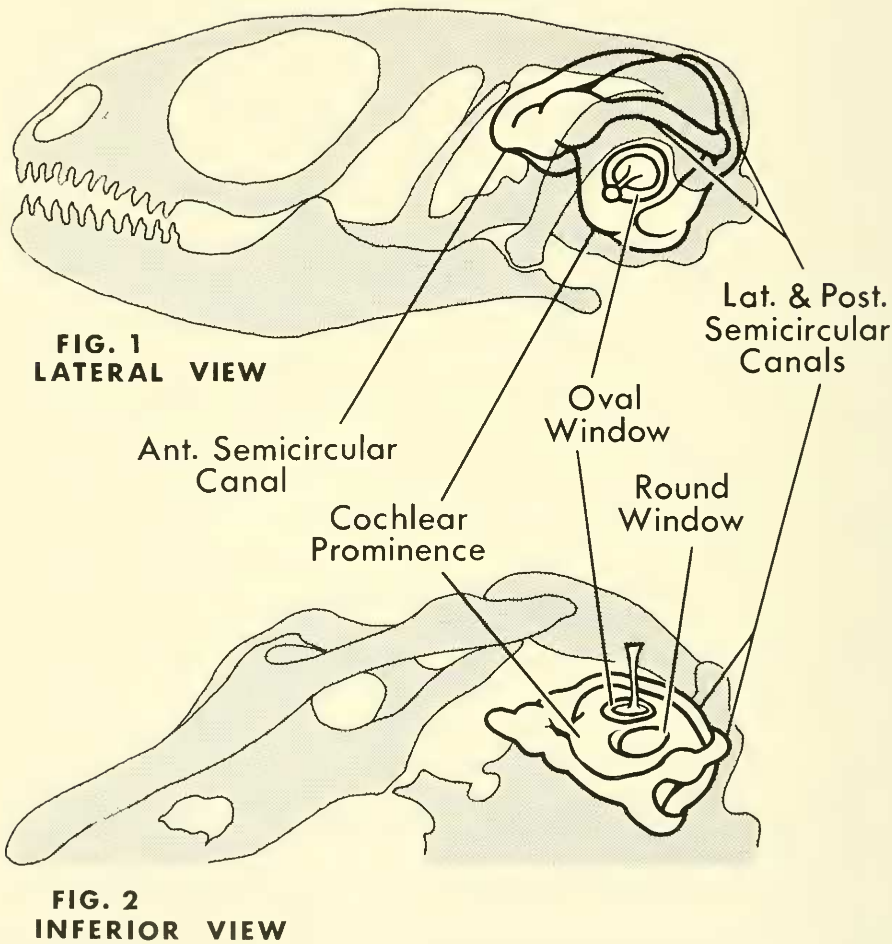


FIGURE 1. Schematic representation of the otic region, *Xantusia*, lateral view.

FIGURE 2. Schematic representation of the otic region, *Xantusia*, inferior view.

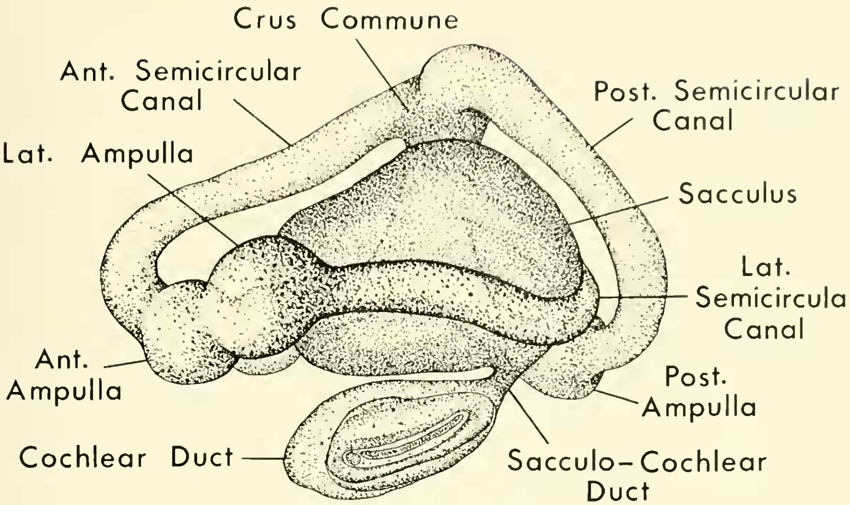


FIG. 3- LATERAL VIEW

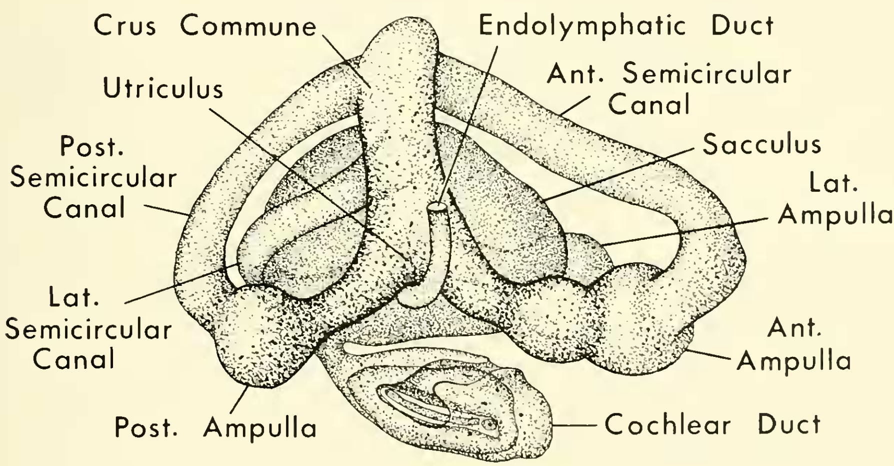


FIG. 4 - MEDIAL VIEW

Figure 3. Left membranous labyrinth, lateral view, *Xantusia vigilis*.

Figure 4. Left membranous labyrinth, medial view, *Xantusia vigilis*.

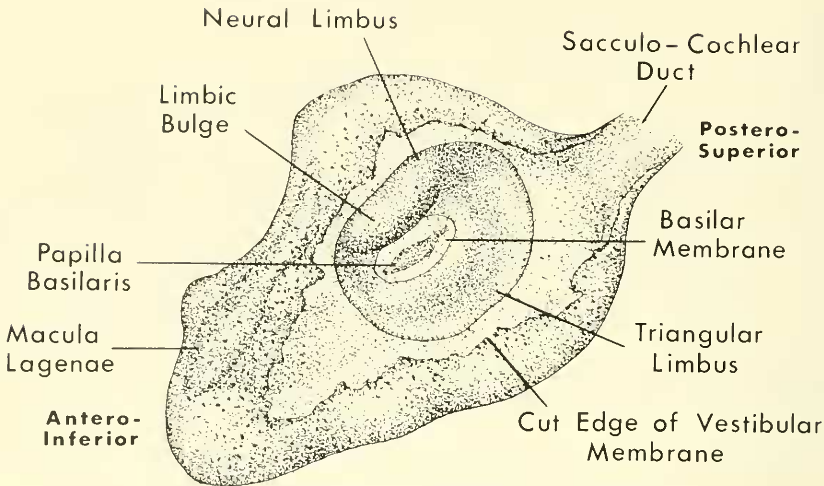


FIG. 5 - LATERAL VIEW

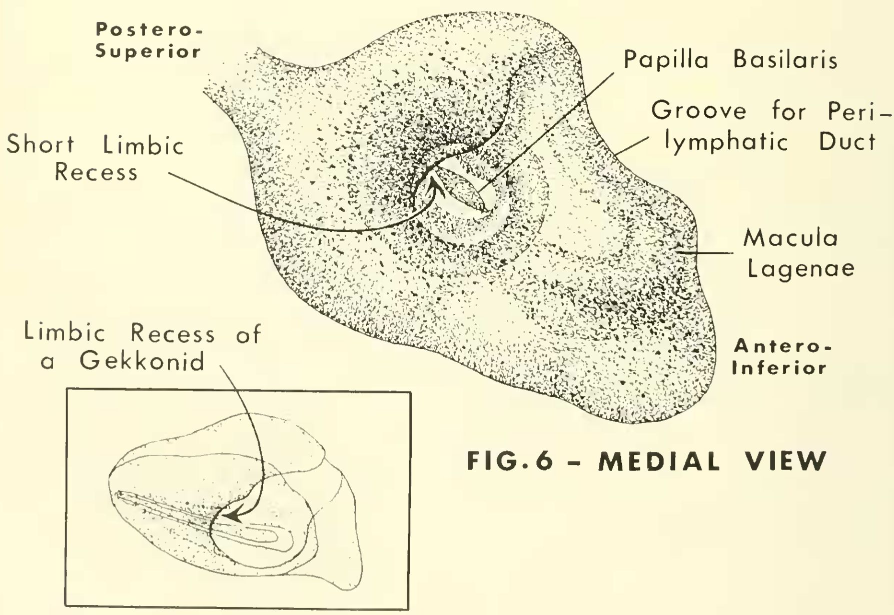


FIG. 6 - MEDIAL VIEW

Figure 5. Cochlear duct, lateral view, *Crotaphytus wislizeni*.

Figure 6. Cochlear duct, medial view, *Crotaphytus wislizeni*.

tissue containing abundant intercellular substance that imparts a flexible quality to this portion of the duct. The supporting tissue is thickened where it surrounds the basilar membrane and is termed the limbus. The anterosuperior portion of the limbus is thicker and larger than the posteroinferior limb and is variously modified and sculptured on both medial and lateral surfaces. Since the auditory nerve is closely apposed to the medial side of the anterosuperior portion of the limbus, it is designated the neural limbus. The lateral surface of the neural limbus may be merely a thin unsculptured plate, be thickened, or may give rise to liplike projections. A tectorial membrane usually arises from the lateral aspect of the neural limbus and overlies the cellular surface of the papilla basilaris.

The medial side of the limbus is differently sculptured in large part to accommodate the perilymphatic duct and sac which conduct sound-pressure waves through the perilymphatic fluid from the perilymphatic cistern to the medial aspect of the basilar membrane (fig. 9). Hamilton (1960, 1964) and Baird (1960a) prefer a different terminology for the various portions of the perilymphatic (periotic) system. Until more extensive studies have been made on the homologies of the structures of the perilymphatic system among different vertebrate groups, I prefer to retain the older terminology.

In some types of cochlear ducts, the perilymphatic sac is not enclosed by any portion of the limbus along the greater part of the medial aspect of the basilar membrane (figs. 6 [not insert], and 8). In other types of ducts, a considerable extent of the basilar membrane on the medial side may be enclosed by connections between the two portions of the limbus (figs. 6 [insert], and 7). Shute and Bellairs (1953) refer to the enclosed area as a limbic recess and the perilymphatic space, a perilymphatic diverticulum. Hamilton (1964) terms the recess, a *furrow*, and that portion of the perilymphatic sac or tympanic scala that extends into this space, an *accessory scala*. For the present, I prefer to use the terminology of Shute and Bellairs (1953).

The posteroinferior part of the limbus is not as much modified as the neural limb (figs. 5, 7, and 8). Because of its approximately triangular shape in cross section it is called the triangular limbus. It should be understood that the limbus is one complete structure varying in shape from a saucer-like plate to an elongated ovoid, and has in its central portion an opening or hiatus across which is stretched the basilar membrane.

Supported on the lateral aspect of the basilar membrane is a thin bar of connective tissue identical in structure to the limbic connective tissue, which in turn supports the papilla basilaris (fig. 7). The limbic hiatus and papilla basilaris vary in size and shape from small circular or ovoid to large elongate structures.

The papilla basilaris may be a simple continuous strip of cells, or may be

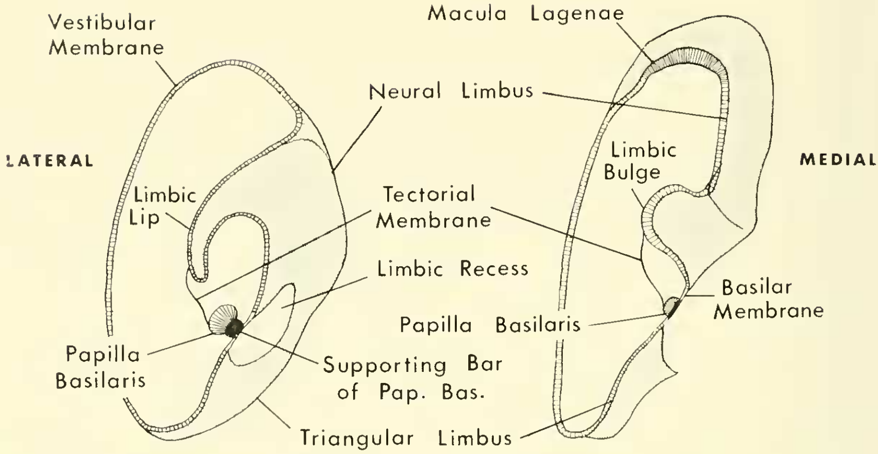


FIG. 7 – Hemidactylus (gekkonid) **FIG. 8 – Sauromalus** (iguanid)

Cross sections of cochlear ducts

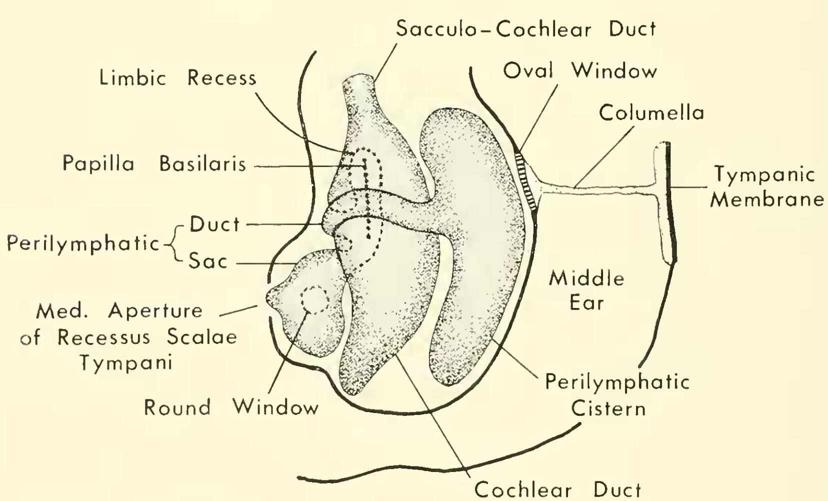


FIG. 9 – Diagrammatic anterior view of left cochlear duct & related structures

FIGURE 7. Cochlear duct, cross section, *Hemidactylus*.

FIGURE 8. Cochlear duct, cross section, *Sauromalus*.

FIGURE 9. Relation of perilymphatic spaces to the cochlear duct.

divided by a limbic connective tissue bar. The papilla may also be evenly contoured, or one end may be widened producing a fusiform-shaped structure.

That portion of the cochlear duct housing the limbus, basilar membrane, and papilla basilaris was termed the *pars basilaris* by Retzius (1884). Since the basilar membrane is only a limited portion of this part of the cochlear duct, I refer to this as the limbic rather than basilar portion of the duct.

The anterosuperior part of the cochlear duct is supported along its anterior edge by the same type of modified connective tissue that makes up the limbus (figs. 5, 6, and 8). This heavy supporting tissue may extend also onto the anterolateral and anteromedial portions of the duct. On the inner luminal surface of this portion of the cochlear duct is a strip of sensory epithelium covered by an otolithic membrane, the macula lagenae. The size and shape of the macula lagenae differs from one lizard family to another. The portion of the cochlear duct housing the macula lagenae may be designated the lagena or lagenar portion of the duct. Reference to figures 5 and 6 and the plates will make it clear, however, that in most lizards, the lagenar and limbic-containing portions of the cochlear duct form a united structure. Thus, while the location of the papilla basilaris and the macula lagenae is definite, there is not a clear-cut distinction between the lagenar and limbic portions of the duct.

B. General Anatomical Characteristics of the Cochlear Duct of Certain Reptilian Orders and Suborders.

1. Order **Rhynchocephalia** (Tuatara) (plate XXI). A striking feature of the cochlear duct of *Sphenodon* is the incomplete fusion between the lagenar and limbic portions of the duct. The duct appears to be made up of two partly joined sacs instead of one completely united structure. There is no specialization of the lateral face of the neural limbus but the medial side is deeply excavated, which imparts a ring or tubular shape to the limbus. The basilar membrane is stretched across the lateral end of the tube-like limbus. Thus, the tubular aspect of the *Sphenodon* limbus is reminiscent of the type of limbus found in amphibians. From this standpoint, the limbus of the *Sphenodon* is more like the amphibian that that of any other reptilian type.

A major difference, however, between the amphibian and *Sphenodon* limbus is the absence in the former of a basilar membrane, and the fact that the papilla basilaris of the amphibian rests on a portion of the limbic wall. The development of a basilar membrane is necessary for direct apposition of the scala tympani to the basilar membrane and appears first in reptiles.

The papilla basilaris seems to be an elongate strip (because of the thickness of the bone of the head, the papilla basilaris was not as perfectly preserved as might be desired). The papilla basilaris is 1.2 mm. and the macula lagenae approximately 2 mm. long (table 2).

TABLE 2. *Snout–vent, cochlear duct, and papilla basilaris length and area in different families of lizards.*

	Snout–Vent (length in mm.)	Cochlear duct (length in mm.)	Papilla basilaris (length in mm.)	(area in mm.^{2})
IGUANIDAE				
Anolis biporcatus	62	1.4	0.60	0.029
Anolis carolinensis	58	1.2	0.45	0.033
Liolaemus pictus	62	1.1	0.30	0.015
Phrynosoma douglassi	78	1.5	0.30	0.017
Tropidurus hispidus	99	1.2	0.35	0.030
Uma scoparia	99	1.0	0.25	0.013
Sauromalus obesus	95	1.8	0.30	0.030
Sceloporus magister	90	1.4	0.35	0.018
Holbrookia texana	65	1.1	0.25	0.011
Iguana iguana	150	2.7	0.60	0.031
AGAMIDAE				
Agama persica	63	1.1	0.30	0.014
Amphibolurus barbatus	140	1.5	0.40	0.026
Calotes versicolor	80	1.2	0.40	0.023
Chlamydosaurus kingi	160	2.2	0.60	0.029
Draco rizali	86	1.4	0.40	0.020
Gonyocephalus grandis	95	1.5	0.60	0.031
Hydrosaurus pustulosus	90	2.4	0.70	0.036
Japalura polygonata	50	1.1	0.30	0.019
Uromastix loricatus	108	2.0	0.25	0.013
CHAMAELEONIDAE				
Brookesia superciliaris	50	1.0	0.15	0.009
Chamaeleo bitaeniatus	72	1.4	0.15	0.011
Chamaeleo brevicornis	80	1.6	0.15	0.013
Chamaeleo diplepis	100	1.6	0.15	0.011
ANGUIDAE				
Anguis fragilis	150	1.2	0.2	0.013
Gerrhonotus multicarinatus	128	1.4	0.4	0.027
Diploglossus lessonae	115	1.8	0.5	0.029
Ophisaurus ventralis	290	1.4	0.3	0.020
Gerrhonotus coeruleus	150	1.2	0.4	0.013
ANNIELLIDAE				
Anniella pulchra	140	1.2	0.2	0.018
XENOSAURIDAE				
Xenosaurus grandis	120	1.9	0.15	0.012
HELODERMATIDAE				
Heloderma suspectum	170	2.4	0.8	0.035
VARANIDAE				
Varanus nuchalis	165	4.0	2.3	0.176
Varanus punctatus	90	1.3	1.0	0.091
Varanus salvator	150	3.6	2.4	0.190
Varanus salvator	120	3.5	2.2	0.138
LACERTIDAE				
Acanthodactylus cantoris	67	1.4	0.40	0.014

Table 2. Continued.

	Snout–Vent (length in mm.)	Cochlear duct (length in mm.)	Papilla basilaris (length in mm.)	Papilla basilaris (area in mm.^{2})
Eremias argus	55	1.4	0.50	0.022
Lacerta viridis	95	1.5	0.60	0.030
Lacerta vivipara	61	1.0	0.36	0.017
Psammodromus algirus	70	1.5	0.60	0.023
Teiidae				
Anadia bogotensis	58	1.0	0.4	0.014
Ameiva ameiva	150	2.4	1.1	
Bachia peruana	70	1.1	0.55	0.022
Dicrodon lentiginosus	53	2.0	0.90	0.046
Cnemidophorus tigris	90	1.9	0.80	0.048
Kentropyx calcaratus	100	1.9	0.90	0.051
Tupinambis teguixin	140	3.4	1.4	0.125
GEKKOTA				
a. Eublepharidae				
Coleonyx species	60	1.2	0.8	0.057
Eublepharus species	90	2.6	1.7	0.115
b. Sphaerodactylidae				
Gonatodes fuscus	40	1.2	0.7	0.072
Sphaerodactylus argus	32	1.2	0.7	0.043
Sphaerodactylus cinereus	34	1.1	0.7	0.052
c. Gekkonidae				
Aristelliger nelsoni	79	2.1	1.2	0.091
Bavayia sauvagii	60	1.8	1.4	0.109
Cosymbotus platyurus	57	1.7	0.9	0.068
Gecko japonica	50	1.7	1.0	0.080
Gehyra multilata	45	1.7	1.1	0.075
Hemidactylus turcicus	55	1.5	0.9	0.046
Microgecko helenae	27	0.9	0.6	0.031
Phyllodactylus bauri	33	1.5	0.9	0.060
Phyllurus cornutus	135	3.8	1.6	0.120
Teratoscincus scincus	90	2.0	1.4	0.084
Gecko gecko	100	3.5	2.0	0.150
Pygopodidae				
Aprasia pulchella	115	0.4	0.25	–
Lialis burtonis	175	2.0	1.4	0.091
Pygopus lepidopodus	150	2.1	1.4	0.103
Scincidae				
Ablepharus lineocellatus	50	1.2	0.75	0.041
Aulacoplax leptosoma	40	1.2	0.8	0.038
Acontias meleagris	110	1.1	0.6	0.053
Brachymeles gracilis	68	1.6	1.0	0.051
Eumeces fasciatus	62	1.5	1.0	0.052
Liolopisma assatum	50	1.4	1.05	0.053
Lygosoma verrauxi	115	1.3	0.7	0.047
Mabuya multifasciata	115	2.0	1.8	0.125
Mabuya multicarinata	80	2.0	1.4	0.077
Nessia monodactyla	80	0.9	0.6	0.040

TABLE 2. Continued.

	Snout Vent (length in mm.)	Cochlear duct (length in mm.)	Papilla basilaris (length in mm.)	Papilla basilaris (area in mm.²)
Sphenomorphus quoyi	75	2.1	1.5	0.118
Tiliqua scincoides	90	2.8	1.9	0.162
Typhlosaurus cregoi	153	1.0	0.6	0.042
FEYLINIIDAE				
Feylinia currori	115	1.2	0.7	0.046
XANTUSIIDAE				
Klauberina riversiana	64	1.9	1.1	0.074
Lepidophyma flavomaculatum	80	1.8	1.2	0.096
Xantusia vigilis	40	1.3	0.7	0.047
Xantusia henshawi	55	1.6	0.9	0.062
CORDYLIDAE				
Cordylus jonesii	60	2.2	1.2	0.064
Cordylus polyzonus	60	2.0	1.1	0.080
Cordylus cordylus	60	2.1	1.2	0.096
Gerrhosaurus flavigularis	160	2.4	1.3	0.108
DIBAMIDAE				
Dibamus argenteus	136	0.8	0.15	0.020
AMPHISBAENIDAE				
Amphisbaena fuliginosa	280	1.8	0.2	0.029
Bipes biporus	180	1.4	0.1	0.008
Blanus cinereus	112	0.5	0.1	–
Diplometopon zarudnyi	130	1.4	0.18	0.010
Rhineura floridana	230	0.9	0.25	0.024
Order CHELONIA				
TESTUDINIIDAE				
Gopherus berlandieri	150	2.5	0.6	0.073
Suborder OPHIDIA				
COLUBRIDAE				
Pituophis catenifer	600	1.5	0.35	0.016
Order CROCODILIA				
Alligator mississippiensis	200 (immature)		4.7	1.32

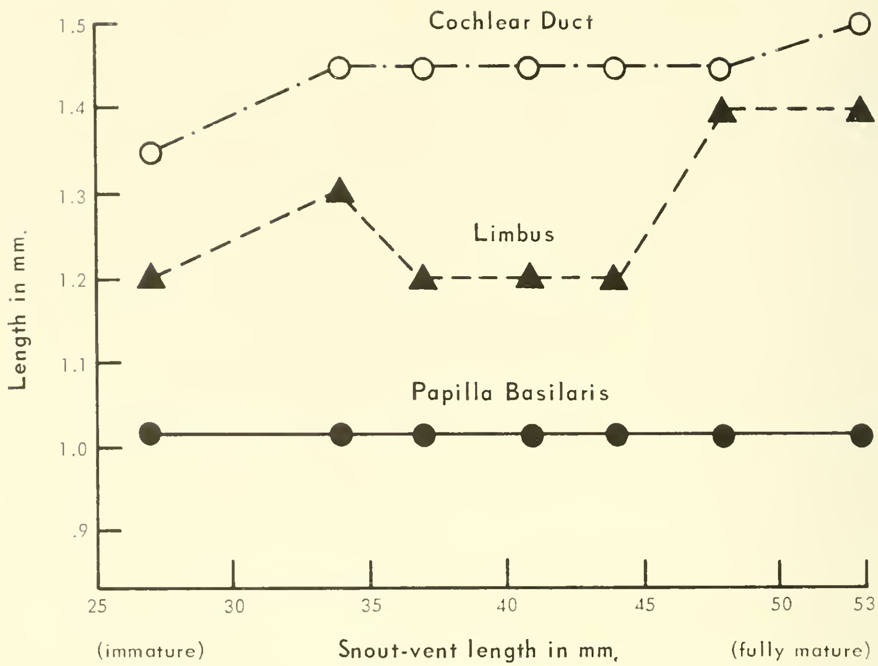
The medial wall of the duct is deeply excavated for reception of the perilymphatic sac and two triangular arms almost close over the perilymphatic duct on the anterosuperior part of the limbus.

2. Order **Chelonia** (turtles and tortoises) (plate XX). While representatives of only four turtle families have been seen (Kinosternidae, Emydidae, Trionychidae, and Testudinidae), the cochlear duct of these types is characterized by fusion of a portion of the saccular wall to the anterolateral aspect of the cochlear duct, a relatively small lagenar sac, lack of limbic specialization, and an ovate papilla basilaris of moderate size (table 2).

3. Order **Serpentes** (snakes) (plate XIX). Representatives of nearly all snake families have been seen. Observations to date indicate some but not outstanding, familial diversity in the cochlear duct of snakes.

TABLE 3. *Variations in the length and width and length/width ratio of the cochlear duct and limbus and variations in the length of the papilla basilaris.*

FAMILY	NO. GEN-ERA	NO. SPE-CIES	COCHLEAR DUCT Length (mm.)	Width (mm.)	(W/L) × 100 (average)	LIMBUS Length (mm.)	Width (mm.)	(W/L × 100) (average)	PAPILLA BASILARIS Length (mm.)	Length in 60–70 mm. specimens
I Iguanidae	28	49	0.9–2.7	0.7– 1.8	54–100(77)	0.6– 1.4	0.4– 1.0	57–100(73)	0.2– 0.75	0.4
II Agamidae	12	17	0.9–2.4	0.8– 1.7	70–114(90)	0.6– 1.7	0.5– 1.3	67–100(81)	0.2– 0.75	0.3
III Chamaeleonidae	2	4	1.0–1.6	0.8– 1.4	57–87 (77)	0.6– 0.75	0.45–0.75	60–100(90)	0.15	0.15
IV Anguidae	4	5	1.2–1.8	0.8– 1.4	67–86 (79)	0.6– 1.1	0.5– 0.7	64–84 (72)	0.2– 0.5	0.4
V Anniellidae	1	1	1.2	1.0	83	0.9	0.7	77	0.2	–
VI Xenosauridae	1	1	1.9	1.8	95	1.0	0.8	80	0.15	–
VII Helodermatidae	1	1	2.4	1.8	75	1.6	1.3	81	0.8	–
VIII Varanidae	1	3	1.3–4.0	0.8– 2.0	50–62 (54)	1.15–3.2	0.7– 1.6	48–61 (53)	1.0– 2.3	–
IX Lacertidae	5	9	1.0–1.5	0.75–1.2	71–83 (79)	0.7– 1.0	0.4– 0.6	50–71 (58)	0.37–0.6	0.4
X Teiidae	10	17	0.9–3.4	0.6– 1.7	50–80 (61)	0.8– 2.2	0.4– 0.8	37–56 (46)	0.4– 1.4	0.75
Gekkonidae										
XI Gekkota–Eublepharidae	23	34	0.9–3.8	0.6– 2.3	47–75 (64)	0.9– 2.2	0.35–1.4	37–67 (51)	0.6– 1.7	1.0
Sphaerodactylidae										
XII Pygopodidae	3	3	0.4–2.1	0.4– 1.6	70–100(82)	0.35–1.8	0.35–0.8	44–100(63)	0.25–1.6	–
XIII Scincidae	24	42	0.8–3.8	0.5– 2.6	46–82 (64)	0.7– 3.2	0.3– 1.8	40–77 (57)	0.6– 2.2	1.0
XIV Feyliniidae	1	1	1.2	0.9	75	1.0	0.6	60	0.7	–
XV Xantusiidae	3	4	1.3–1.9	0.6– 1.1	46–61 (51)	1.1– 1.7	0.5– 1.0	43–59 (49)	0.7– 1.2	1.0
XVI Cordylidae	2	4	2.0–2.4	1.0– 1.4	60–64 (62)	1.6– 2.0	1.0	50–63 (60)	1.1– 1.4	1.15
XVII Dibamidae	1	1	0.8	0.5	63	0.6	0.4	75	0.15	–
XVIII Amphisbaenidae	5	5	0.5–1.8	0.4– 0.95	43–80 (64)	0.3– 0.6	0.3– 0.6	83–100(96)	0.1– 0.3	–
XIX Shinosauridae	Not seen									
XX Anelytropsidae	Not seen									
XXI Lanthanotidae	Not seen									

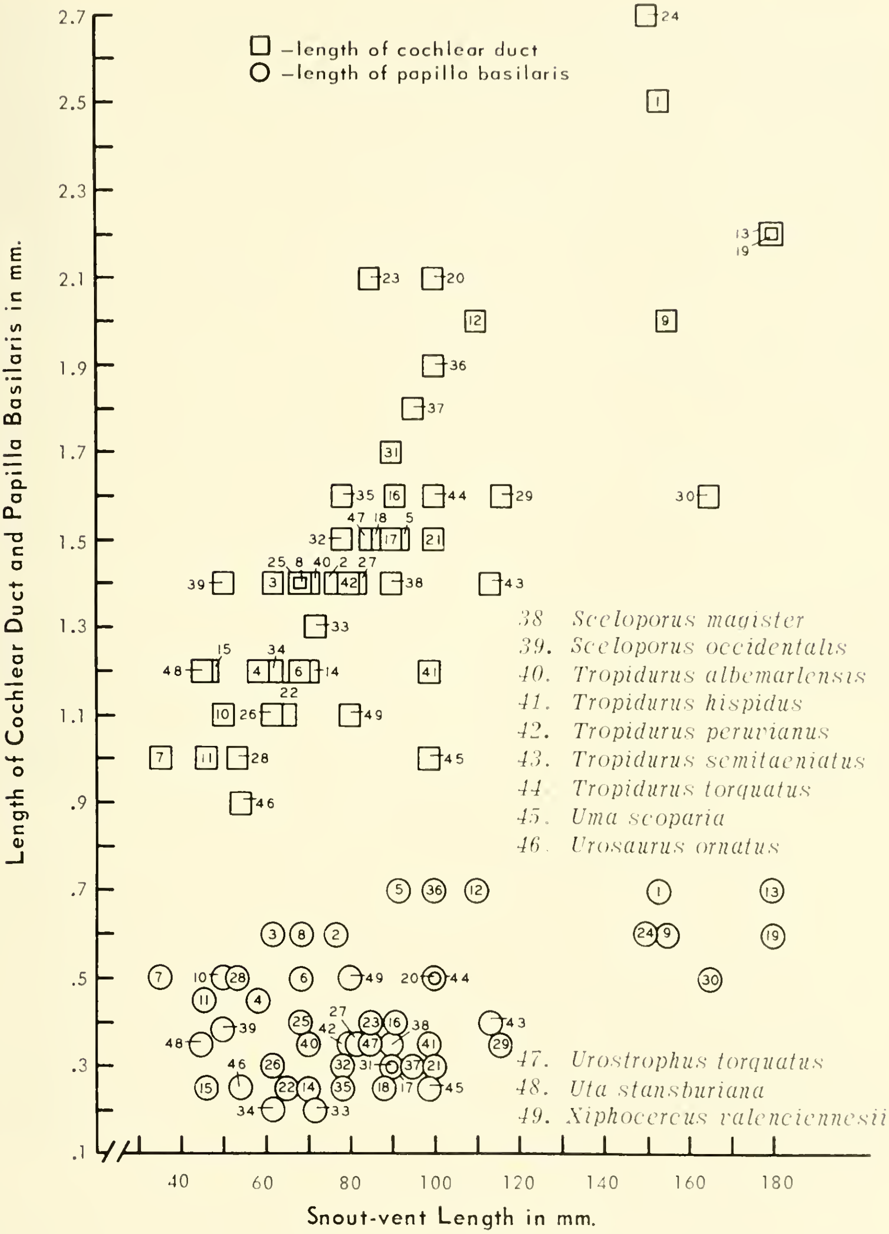


GRAPH 1. Changes in the length of the cochlear duct, limbus, and papilla basilaris during growth of the scincid lizard, *Leiolopisma assatum*.

→

1. *Amblyrhynchus cristatus*
2. *Anolis antiquae*
3. *Anolis biporcatus*
4. *Anolis carolinensis*
5. *Anolis copei*
6. *Anolis cristatellus*
7. *Anolis cupreus*
8. *Anolis distichus*
9. *Anolis equestris*
10. *Anolis polylepis*
11. *Anolis sallaei*
12. *Basiliscus vittatus*
13. *Brachylophus fasciatus*
14. *Callisaurus draconoides*
15. *Chalarodon madagascariensis*
16. *Corythophanes hernandezii*
17. *Crotaphytus collaris*
18. *Crotaphytus wislizeni*
19. *Ctenosaura pectinata*
20. *Ctenosaura similis*
21. *Dipsosaurus dorsalis*
22. *Holbrookia texana*
23. *Hoplocercus spinosus*
24. *Iguana iguana*
25. *Leiocephalus carinatus*
26. *Liolaemus pictus*
27. *Mariguana agassizi*
28. *Norops auratus*
29. *Oplurus cuvieri*
30. *Petrosaurus thalassina*
31. *Phrynosoma coronatum*
32. *Phrynosoma douglassi*
33. *Phrynosoma m'calli*
34. *Phrynosoma modestum*
35. *Phrynosoma platyrhinos*
36. *Plica plica*
37. *Sauromalus obesus*

GRAPH 2. Relation between the snout-vent length and cochlear duct and papilla basilaris length in the Iguanidae.



Graph 2. Relation between the snout–vent length and cochlear duct and papilla basilaris length in the Iguanidae.

Like *Sphenodon*, the snake cochlear duct shows incomplete fusion between the lagenar and limbic portions. Whereas in *Sphenodon*, turtles, and most lizards, the limbic portion of the cochlear duct is larger than the lagenar, in snakes, the lagenar sac is considerably larger than the limbic area. There is no marked modification of the lateral wall of the neural limbus, and the medial limbic wall shows no extensive recesses. The papilla basilaris is ovoid to slightly elongate and small in its dimensions (table 2).

4. Order **Sauria** (lizards). In this order I have seen the cochlear ducts of approximately 39 per cent of the living genera (131 of approximately 334 genera), representing 18 families. The most striking feature of the lizard cochlear duct is that it is anatomically distinct for each family and shows considerable modifications of its constituent elements.

General anatomical characteristics of the lacertilian cochlear duct are: (a) usually complete fusion between the lagenar and limbic portions; (b) a limbic portion usually equal to or larger than the lagenar; (c) modification of the neural limbus; (d) a papilla basilaris varying markedly in length and shape; (e) a basilar membrane variously open or closed by the limbus on the medial aspect; and (f) except for the skinks, no marked tendency for bending or coiling of the duct.

5. Order **Crocodilia**. I have seen the cochlear duct of *Alligator mississippiensis*. The duct is considerably elongated and has a half turn or twist. The lagenar area is reduced to a small dilation at the inferior tip of the duct. The papilla basilaris is at least twice as long and its surface area is much greater than that of other reptiles (table 2). There are other modifications of the perilymphatic cistern, duct, and sac but these will not be described in this paper.

C. Anatomical Characteristics of the Cochlear Duct of Lacertilian Families.

The families of lizards are arranged according to my present concept of an increasing degree of complexity of the cochlear duct, except that I treat the dibamids and amphisbaenids last as their relationships are not clear at this time.

1. **Iguanidae** (plate I; graph 2). While the iguanids and agamids show many cochlear duct features in common, nevertheless they each possess distinctive cochlear features. I believe that the duct types found in the members of these two families are generalized or relatively unspecialized.

Features of the iguanid cochlear duct:

a. The cochlear duct is pyramidal in shape, the base broad, and the inferior tip usually pointed, although occasionally rounded. Medial bending of the inferior tip is not marked, but may be prominent in some species. The duct is not as square as is that of the agamid, and not as elongate as that of many other families (see length-width ratios in table 3). The length of the cochlear duct varies directly with the snout-vent length of the species (graph 2).

b. The macula lagenae is large, begins high anterosuperiorly, and runs down the anterior surface of the duct, and at its inferior extremity curves medially. The macula lagenae is two to three times the length of the papilla basilaris.

c. The limbus is ovoid to moderately elongate. Elongation is more marked in the anolids. The neural limbus has a moderate bulge on its lateral face that is bar- or rolling-pin-like in appearance. In the tropidurid iguanids, the neural bar is more undercut than in other iguanids, a feature similar to the agamid lateral neural limbus.

d. In most species, the anterior edge of the duct has only a shallow groove for the perilymphatic duct, while in large species with large ducts, the perilymphatic duct groove is deepened.

e. The medial aspect of the basilar membrane is almost entirely open, but in some species short shallow limbic recesses are present both superiorly and inferiorly. The medial limbic flanges housing the auditory nerve and perilymphatic duct are not prominent.

f. The papilla basilaris is relatively short but increases in length and area in the anolids (table 2 and graph 2). There is not as close a correlation between species size and papilla basilaris length as there is in some other lizard families (compare graphs 2 to 8). The length of the papilla basilaris therefore is probably associated with specific differences other than that of size.

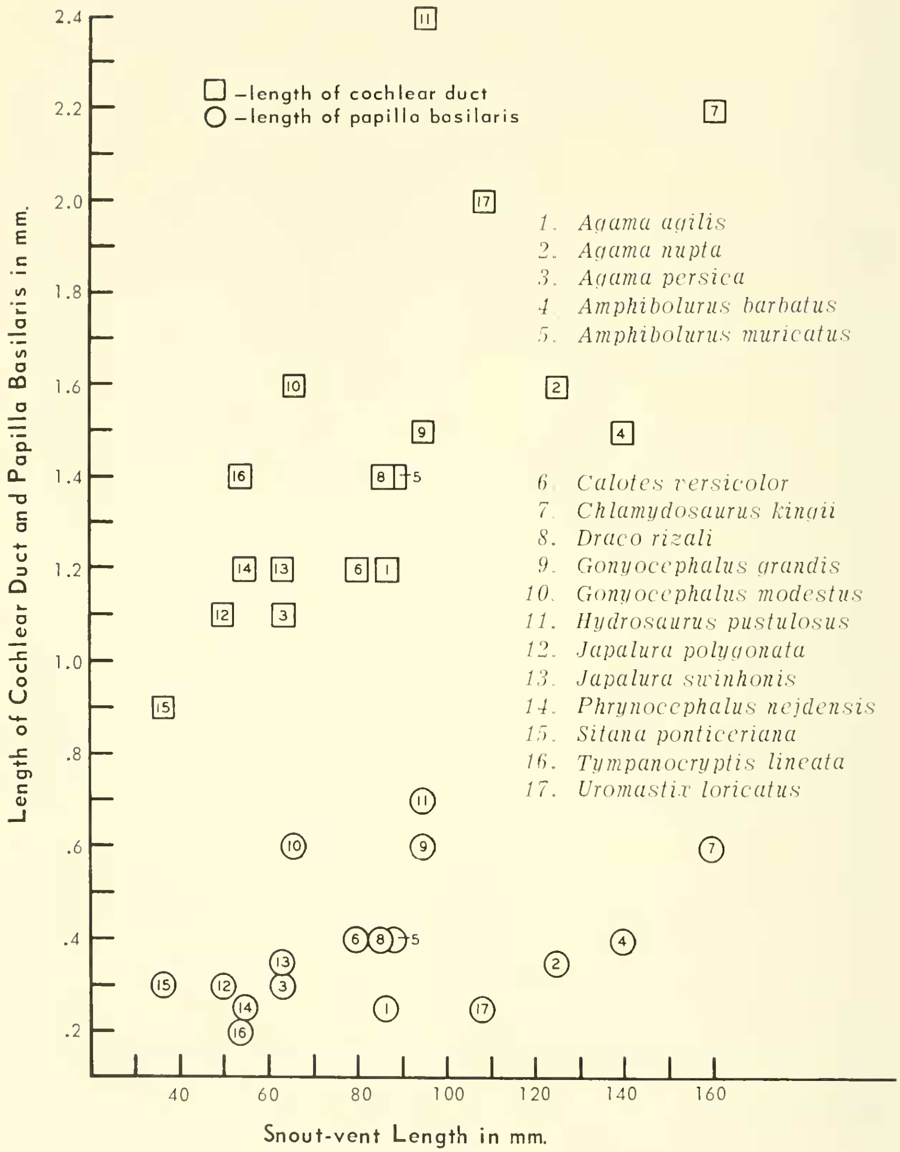
While a detailed analysis of generic differences will be reported in a later paper, a few general observations are noted here. Compared with other iguanids, the limbus and papilla basilaris is longer in anolids; the cochlear duct is more pointed and elongated, and the neural limbic bar better developed in the tropidurids and in *Plica plica*; the neural limbic bar is more prominent in *Sauromalus obesus*; and the limbus and papilla basilaris are relatively short and small in the "earless" lizard, *Holbrookia texana*.

2. **Agamidae** (plate II; graph 3).

a. The cochlear duct is nearly as broad as long and is shaped like a right triangle with the right angle at the posterosuperior corner. The inferior tip is rounded and blunt. There is some correlation between cochlear duct and papilla basilaris length and species size, but there is not as close a correlation as is found among genera in other families.

b. The lagena is relatively large and the macula lagenae two to three times the length of the papilla basilaris.

c. The lateral side of the neural limbus is thickened giving rise to a prominent bar which is more pronounced than the type found in the iguanids, but not as marked as that of the anguids, lacertids, or teiids. The triangular limbus is flared posterosuperiorly.



GRAPH 3. Relation between the snout-vent length and cochlear duct and papilla basilaris length in the Agamidae.

d. The groove for the perilymphatic duct varies from shallow to deep, being deeper in large species with larger and more stoutly constructed ducts.

e. The medial face of the basilar membrane is mostly unenclosed, but there are short superior and inferior limbic recesses. The medial limbic flanges are not prominent.

f. The papilla basilaris is relatively short, either elongate or fusiform, and the enlarged end superior in location. The papilla varies from 0.2 mm. to 0.4 mm. in length; there is some tendency for it to be longer and greater in surface area in larger species (graph 3 and table 2).

While the number of agamid genera so far studied is not large, there is a tendency for the shape of the lagena to vary from genus to genus; in *Sitana ponticeriana*, the lagena is reduced in size, in *Tympanocryptis lineata*, the anterior edge of the cochlear duct, instead of being curved, is straight and set at an angle of 45 degrees to the papilla basilaris. And while a blunt or rounded inferior tip is an agamid characteristic, in *Agama persica* (but not *Agama agilis* or *Agama nupta*), the tip is pointed.

3. **Chamaeleonidae** (plate III).

a. The cochlear duct is characteristically triangular, the length approximately 25 per cent greater than the width. The lagenar and limbic portions form a single unit showing no tendency to separation.

b. The macula lagenae is moderate in size.

c. The limbus is thin and saucer-like in shape. The lateral side of the neural limbus shows only the slightest elevation. The limbic hiatus is relatively large and is circular in outline.

d. The groove for the perilymphatic duct is definite but shallow.

e. The medial aspect of the basilar membrane is open.

f. The papilla basilaris is small and circular to slightly ovoid in shape. There is no indication of variation in papilla size with species size (table 2). An insufficient number of species have been studied to know if there are intrafamilial differences.

4. **Anguidae** (plate IV).

a. The cochlear duct is moderately elongate.

b. The lagenar part of the cochlear is moderate in size and the macular length about twice that of the papilla basilaris.

c. The limbus is ovoid and the central hiatus of good size. The lateral side of the neural limbus shows a prominent projection which is longer than the papilla. The neural limbic projection is much more prominent than that found in the iguanids or agamids, but not quite as well developed nor as shelf-like as that of the lacertids. Because of the development of very elongate body types in the anguids, it is difficult to correlate species size with cochlear duct dimensions.

d. The medial side of the limbus has two quite prominent flanges which partially house the perilymphatic duct. This feature is best developed in the gerrhonotids.

e. The medial face of the basilar membrane is mostly open, but there are short inferior and superior limbic recesses.

f. The papilla basilaris is elongate and modest in its dimensions. In most species there is a small area at the inferior extremity of the papilla that apparently lacks hair cells. In both *Ophisaurus ventralis* and *Anguis fragilis*, the total length of the cochlear duct as well as the length of the macula lagenae and the length and area of the papilla basilaris are relatively small (table 2). This is probably the result of regression or degeneration.

5. **Anniellidae** (plate V).

a. The cochlear duct is somewhat square in shape.

b. The lagenar area is reduced in relation to the limbic portion, and it is probable that the cochlear duct has been shortened largely by a decrease in the dimensions of the lagenar area.

c. The limbus is thin, concave, and eccentrically ovoid. The limbic hiatus is quite large which may be characteristic of either a primitive or a reduced condition. A small bar-like limbic lip forms the anterior edge of the neural limbus. The relative distance of the lip from the papilla basilaris gives the appearance that the neural lip has been displaced in position.

d. The groove for the perilymphatic duct on the medial side of the cochlear duct is narrow and shallow.

e. The medial aspect of the basilar membrane is small and entirely open.

f. The papilla basilaris is ovoid and small (table 2).

6. **Xenosauridae** (plate VI).

a. The cochlear duct appears tall because of the relatively large area above (anatomically dorsal to) the limbus proper. Measurements of the cochlear duct show it to be approximately equal in length and width.

b. The lagenar area is mildly constricted from the limbic portion, a possible result of degeneration of the limbus in this family. The macula lagenae is of moderate size and extent.

c. The limbus is relatively small and almost flat on its lateral face except that there is a moderate elevation at the anterior border adjacent to the lagenar portion. There is no apparent modification of the neural limbus.

d. The groove for the perilymphatic duct is quite deep both anterosuperiorly and on the medial surface of the duct.

e. The medial face of the basilar membrane is open.

f. The papilla basilaris is very small (table 2).

7. **Helodermatidae** (plate VII).

a. The cochlear duct is triangular, and the limbic portion quite large.

b. The lagenar area is less than the limbic, but the macula lagenae is of moderate proportions.

c. The limbus is quite thick. The neural limbus presents a rounded prominence that is more massive than the iguanid lip, and different from the anguid in not being sharply undercut just above the basilar membrane.

d. and e. The groove for the perilymphatic duct and sac is large and shallow and the medial aspect of the basilar membrane mostly open. A short limbic recess is present at the superior end of the basilar membrane.

f. The papilla basilaris is probably elongate (my specimen was not perfectly preserved); it is longer than that found in either the anguid or iguanid lizards (table 2). The nerve supplying the papilla basilaris is bifid, but the papilla does not appear to be divided into two segments.

8. **Varanidae** (plate VIII).

a. The cochlear duct is large and elongated (approximately twice as long as wide); the greater length is due to the large, heavily constructed limbus.

b. The pars lagena is of moderate proportions and the macula lagenae a wide strip covering the anterolateral, anterior, and anteromedial aspect of the lagena.

c. The limbus appears massive and may have a small narrow central bridge dividing the limbic hiatus into two unequal portions. The superior end of the divided hiatus is about twice the length of the inferior portion. In specimens with an undivided hiatus, there is a narrowing of the hiatus in the same area where it is divided in others. Two of my four specimens have a divided hiatus and papilla, and two do not. The lateral face of the neural limbus does not show a definite projection, but is thickened in its midportion above each part of the divided limbic hiatus.

d. The groove for the perilymphatic duct is quite deep.

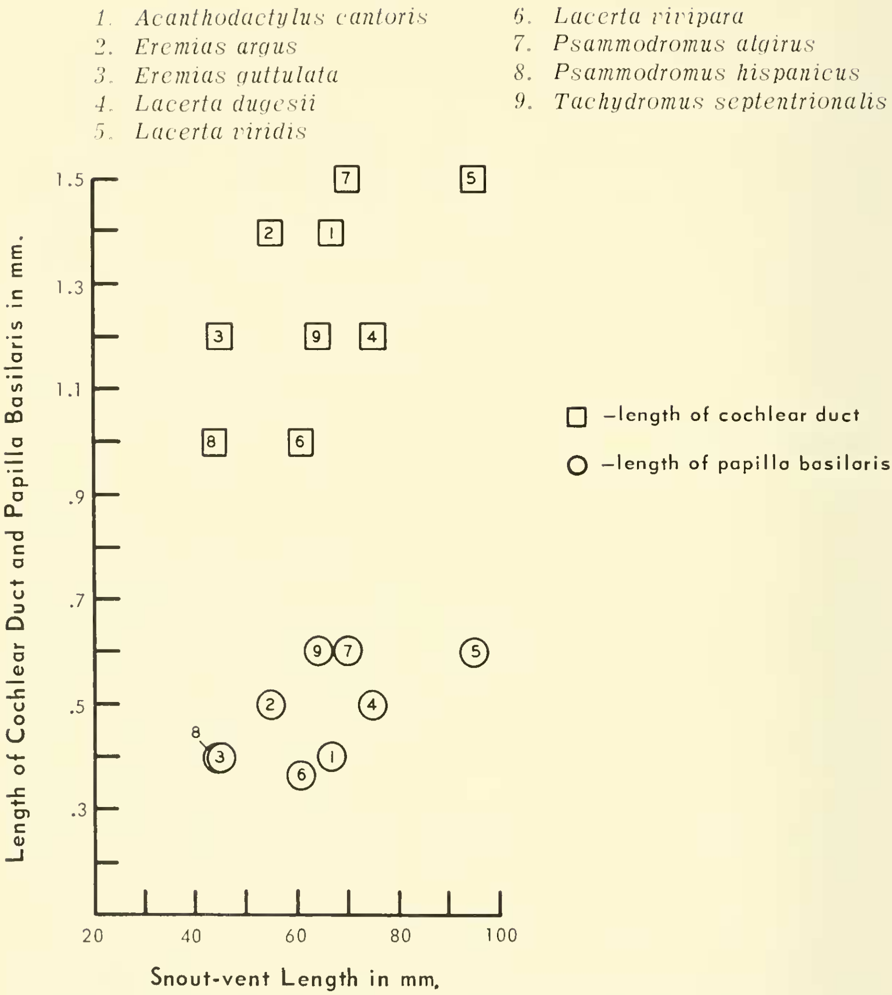
e. The medial face of the basilar membrane is about two-thirds open; a superior limbic recess covers the upper half of the superior portion of the membrane, and a shorter inferior recess covers only 5 to 10 per cent of the inferior part.

f. The papilla basilaris is elongate and may be divided into two unequal portions; the superior part is about twice the length of the inferior. The papilla may or may not be divided. The length of both the cochlear duct and the papilla basilaris is directly related to the size of the species (table 2).

9. **Lacertidae** (plate IX).

a. The cochlear duct is characteristically triangular and the limbic portion markedly posterior (caudal) as well as superior in position.

b. The lagenar portion of the cochlear duct is relatively large and has a



Graph 4. Relation between the snout–vent length and cochlear duct and papilla basilaris length in the Lacertidae.

long superior–inferior axis and tends to extend more superiorly than it does in other families. The macula lagenae is correspondingly long, courses down the entire anterior border of the duct, and extends onto the inferior medial wall.

c. The limbus is ovoid–elongate and characterized by a medial bar or bridge dividing the limbic hiatus into two approximately equal halves. The neural lip is a prominent ridge more marked than that of the anguids, but not as well developed as that of the teiids (compare plates IV, IX, and X).

d. The groove for the perilymphatic duct is shallow.

e. The medial face of the basilar membrane is not enclosed and the excavation for the perilymphatic sac relatively deep. Very short superior and inferior limbic recesses are present.

f. The papilla basilaris is divided into two almost equal portions. Each part is slightly fusiform but elongate in shape. The papilla basilaris is both fairly short in length and small in area and seems to vary directly with species size (table 2 and graph 4). Among the lacertid genera studied, there are minor variations in the thickness and shape of the limbic lip, and the exact shape of the lagena.

10. **Teiidae** (plate X).

a. The cochlear duct is elongate. The posterosuperior curve of the limbus projects dorsally and more superiorly than the corresponding lagenar edge. The inferior tip of the duct is pointed and curves sharply in a medial direction. The teiid cochlear duct has expanded both superiorly and inferiorly; the teiids therefore, differ from the gekkonids, in which group the duct expands superiorly, and from the scincids where the duct expands inferiorly and medially.

b. The lagenar portion of the duct is large and well developed; it forms a robust anterior edge. The macula lagenae is always longer than the papilla basilaris.

c. The limbus is one of the most elongate found in the lizards, the length/width ratio being 46 per cent (table 3). The limbic hiatus is long and narrow. The lateral face of the neural limbus has a rather heavy umbrella-like projection in the middle 50–60 per cent of its length. The neural limbic lip is considerably shorter and much less delicate and projecting than that of the Gekkota and pygopodids.

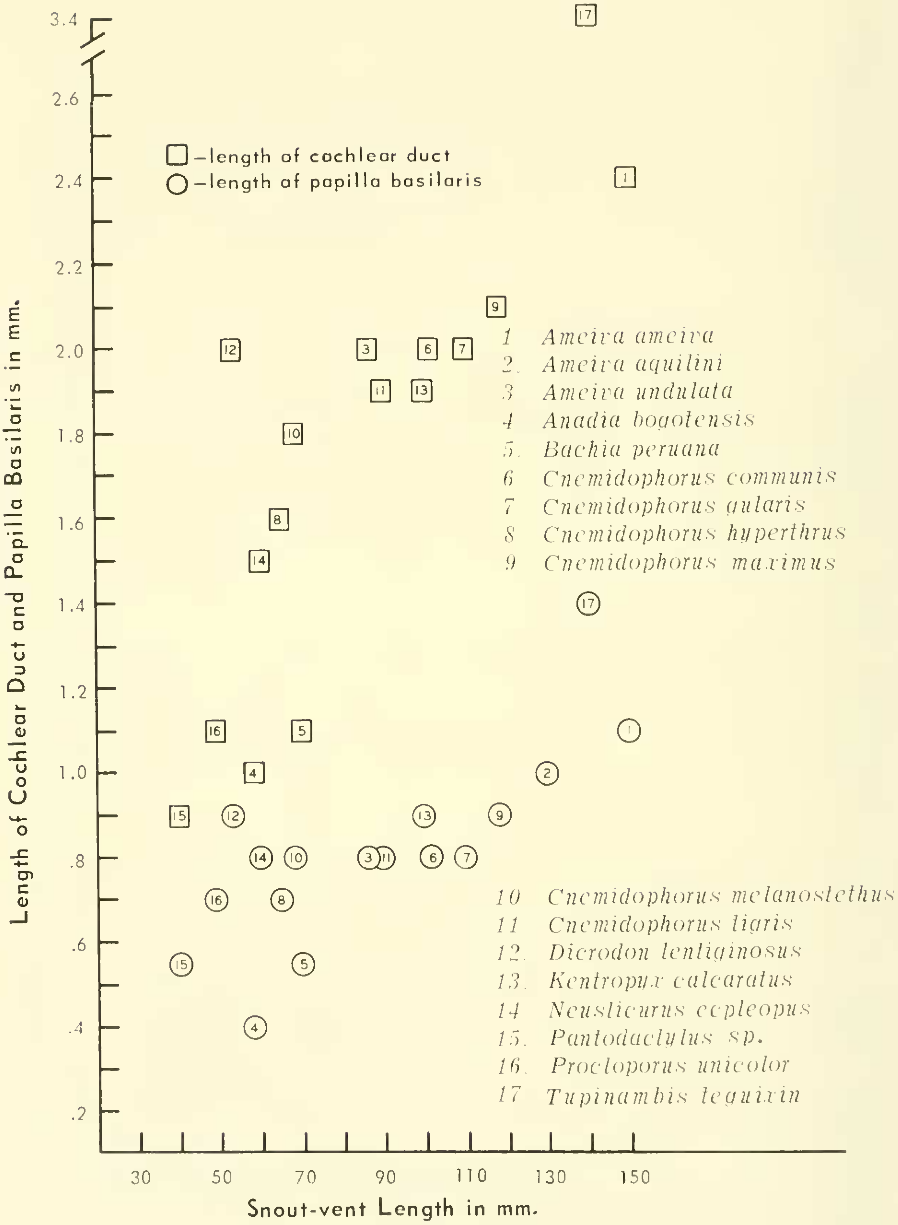
d. The groove for the perilymphatic duct is not well marked.

e. The medial face of the basilar membrane is not enclosed and receives a widely expanded perilymphatic sac.

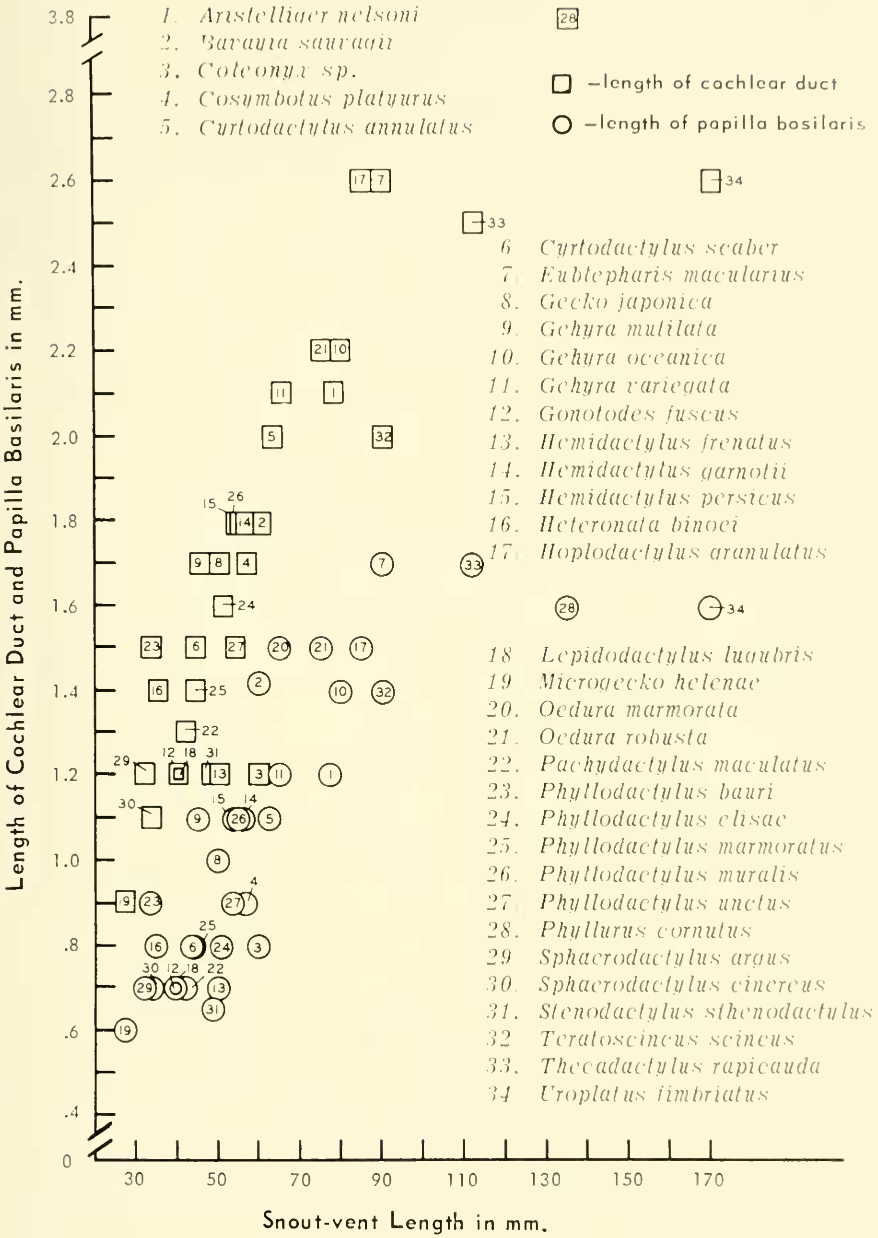
f. The papilla basilaris is moderately long and varies in length and area with the size of the species (table 2 and graph 5). The papilla is slightly expanded inferiorly, and narrowed superiorly. There is usually a break in the papilla basilaris toward the superior tip and the papilla is thus unequally divided with a very short superior portion barely separated from a much longer inferior strip. There is no limbic bridge, however. The tendency towards division of the papilla, together with the development of a thick umbrella-like limbic lip and an open medial basilar membrane are conditions very similar to that found in the lacertids.

Most teiids have robust cochlear ducts, but the microteiids (*Anadia*, *Bachia*, *Pantodactylus*, and *Proctoporus*) show considerable reduction in both the limbic and lagenar portions of the duct.

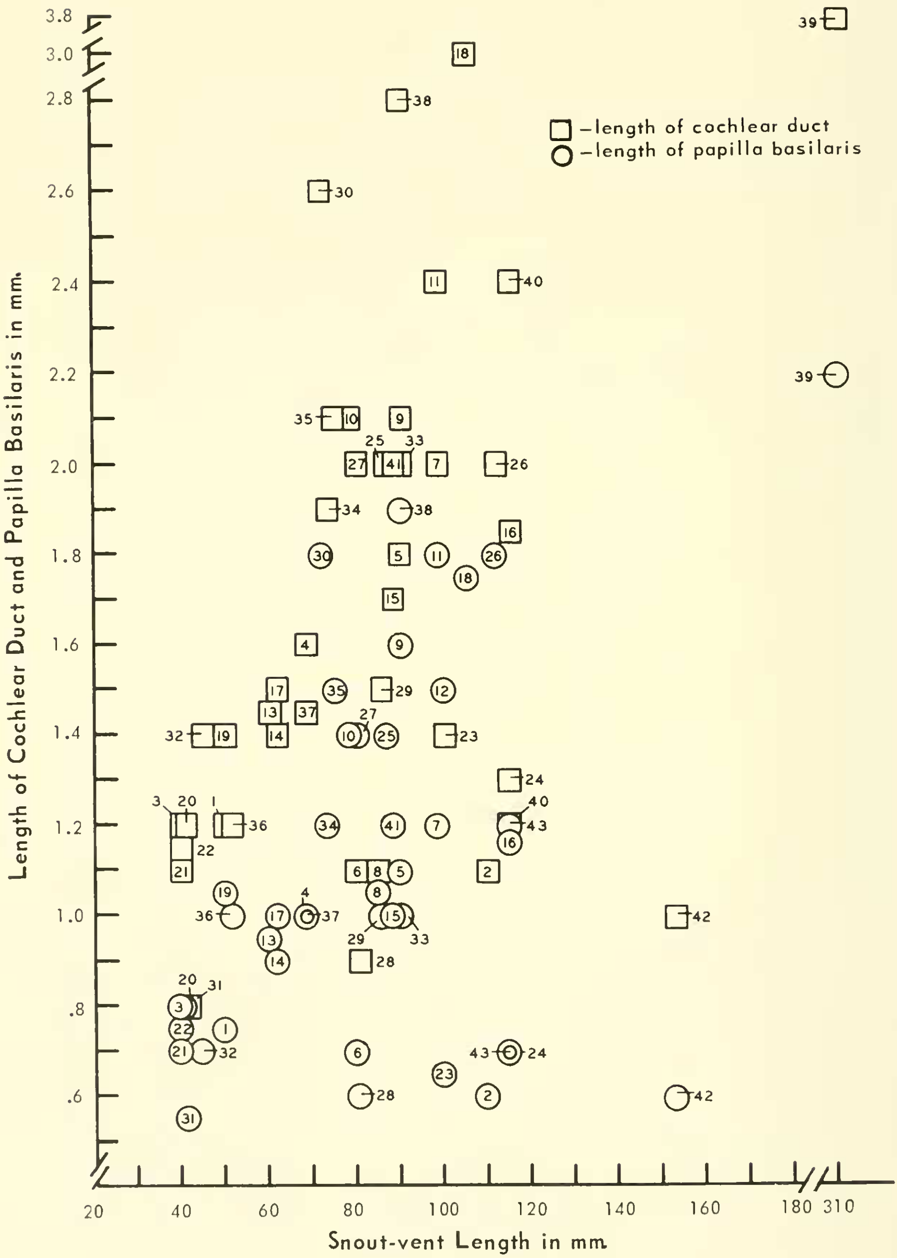
11. **Gekkota** (including **Gekkonidae, Eublepharidae, Sphaerodactylidae,** and **Uroplatidae**) (plate XI; graph 6).



Graph 5. Relation between the snout-vent length and cochlear duct and papilla basilaris length in the Teiidae.



GRAPH 6. Relation between the snout-vent length and cochlear duct and papilla basilaris length in the Gekkota.

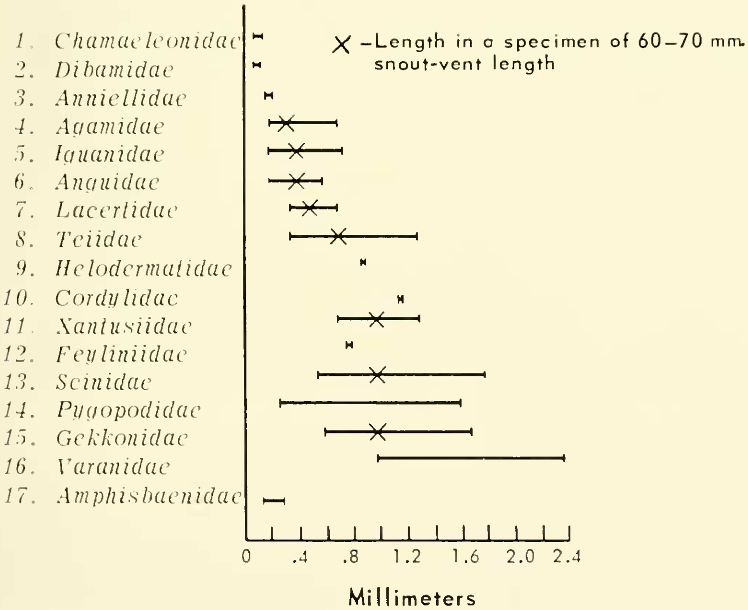


GRAPH 7. Relation between the snout-vent length and cochlear duct and papilla basilaris length in the Scincidae.

1. *Ablepharus lineocellatus*
2. *Acontias meleagris*
3. *Aulacoplax leptosoma*
4. *Brachymeles gracilis*
5. *Brachymeles schadenbergi*
6. *Brachymeles tridactylus*
7. *Chalcides polylepis*
8. *Chalcides sepoides*
9. *Dasia smaragdinum*
10. *Egernia nitida*
11. *Egernia striolata*
12. *Emoia nigra*
13. *Eumeces elegans*
14. *Eumeces stimpsonii*
15. *Eumeces gilberti*
16. *Eumeces obsoletus*
17. *Eumeces fasciatus*
18. *Hemisphaerodon gerrardi*
19. *Leiolopisma assatum*
20. *Leiolopisma guichinoti*
21. *Leiolopisma noctua*
22. *Lygosoma laterale*
23. *Lygosoma lentiginosus*
24. *Lygosoma verrauxi*
25. *Mabuya mabouia*
26. *Mabuya multifasciata*
27. *Mabuya multicarinata*
28. *Nessia monodactyla*
29. *Ophiomorus tridactylus*
30. *Otosaurus cumingi*
31. *Rhodona fragilis*
32. *Riopa bowringii*
33. *Scincus philbyi*
34. *Sphenomorphus indicus*
35. *Sphenomorphus quoyi*
36. *Sphenomorphus tenuis*
37. *Sphenomorphus variegatus*
38. *Tiliqua scincoides*
39. *Trachysaurus rugosus*
40. *Tribolonotus gracilis*
41. *Tropidophorus rivularis*
42. *Typhlosaurus cregoi*
43. (*Feyliniidae*) *Feylinia currori*

←

Graph 7. Relation between the snout–vent length and cochlear duct and papilla basilaris length in the Scincidae.



Graph 8. Range in length of the papilla basilaris in lizard families.

So far I have not studied a sufficient number of eublepharids and sphaerodactylids to state whether they differ significantly from the gekkonids in cochlear duct characteristics. For the present, I will discuss the Gekkota as a whole.

a. The cochlear duct is relatively large and heavy in appearance. The limbic portion has expanded in a posterosuperior direction and pushed into the saccular area. The pars lagena is also prominent and occupies the anteroinferior portion of the duct. The general form of the duct is elongate, and the inferior tip somewhat pointed.

b. The large macula lagenae lies at an angle of approximately 30 to 40 degrees to the papilla basilaris, whereas in the lacertid–teiid complex, the macula lagenae lies more nearly parallel to the papilla. The most notable difference between the basically similar gekkonids and pygopodids is that the macula lagenae and papilla basilaris are parallel to one another in the pygopodids. (Compare plates XI and XII.)

c. The limbus is large and ovoid–elongate (table 3) and its most outstanding feature is the extension from the neural limbus of a thin awning-like projection curving out over the papilla basilaris. This lateral neural limbic projection is much thinner and more delicate as well as relatively greater in extent than the teiid and lacertid limbic lips.

d. The anteroinferior edge of the cochlear duct is frequently deeply grooved by the perilymphatic duct.

e. Only the inferior third of the basilar membrane is open medially as a long limbic recess houses the superior two-thirds of the membrane.

f. The papilla basilaris is an elongate slightly fusiform structure. The thicker end lies inferiorly and there is no tendency for the papilla to be divided. The length and area of the papilla usually varies directly with the size of the species (table 2 and graph 6).

There is less variation in the cochlear duct of the Gekkota than in any other group of lizards. In fact, the constancy of anatomical detail is remarkable. Only in very small species such as *Heteronata binoei*, *Microgecko helenae*, and *Sphaerodactylus argus* is the size of the lagenar and limbic areas much reduced. The reduced size of the limbus and lagena in these small species results in a miniaturized and not a degenerate structure.

The cochlear duct of *Uroplatus fimbriatus* differs only in having a somewhat enlarged lagena.

12. **Pygopodidae** (plate XII).

a. The pygopodid cochlear duct is very similar to the gekkonid duct in that it is elongate, heavy, and superiorly expanded. It differs from the gekkonid duct in that the macula lagenae is more parallel to the papilla basilaris. Also, the inferior tip of the pygopodid duct is more rounded. An insufficient number of pygopodid species have been studied to determine cochlear duct and species size relationships.

b. While in the gekkonids, the macula lagenae is usually longer than the papilla basilaris, in the pygopodids, the macula lagenae is usually shorter.

c. The limbus is elongate, superiorly expanded, and the neural limbus bears a delicate awning-like expansion almost identical to that of the gekkonids.

d. The groove for the perilymphatic duct is of moderate depth.

e. As in the gekkonids, the inferior portion of the medial face of the basilar membrane is open and the superior three-quarters enclosed.

f. The papilla basilaris is very slightly fusiform and tapers towards the superior end. Although too few species were studied to be certain, it is probable that the length of the papilla basilaris varies with the size of the species (table 2). The cochlear duct, macula lagenae, and papilla basilaris are reduced in size (miniaturized) in *Aprasia pulchella*.

13. **Scincidae** (plate XIII).

a. The cochlear duct is relatively large and elongate. The limbic portion is relatively much larger than the lagenar. The limbus has expanded inferiorly rather than superiorly as it does in the gekkonids. The limbus also extends medially and is curved or bent in many species. The overall length of the cochlear duct is largely a function of species size (table 2).

b. While the pars lagena is reduced in size, the length of the macula lagenae is not greatly affected. The macula is almost equal in length to the papilla basilaris and is inclined at an angle of 30 to 40 degrees relative to the papilla.

c. The limbus is relatively thick and has an elongate hiatus. The lateral face of the neural limbus does not have a projection like that of many other lizards, but possesses a moderate ridgelike bulge. In agreement with Hamilton (1964) I have so far been unable to demonstrate without doubt the presence of a tectorial membrane in skinks. Overlying the inferior tip of the papilla basilaris is a thickening which is readily apparent on gross observation. On section, this thickened material has an unstructured appearance and stains basophilically; it might be that this is the remnant of the tectorial membrane that somehow was pulled away from its normal site of origin during development.

d. The groove for the perilymphatic duct varies from deep to shallow.

e. The perilymphatic duct sweeps anterosuperiorly over the medial side of the cochlear duct. The superior 40 per cent of the basilar membrane is open, and the inferior 60 per cent enclosed, housing a long limbic recess. The inferiorly directed limbic recess of the skinks is, thus, the opposite of the superiorly directed recess of the gekkonids. This is another reflection of the supposition that the scincid duct developed by inferior, and the gekkonid, by superior growth. Also related to the direction of duct growth is the reduction in size of the gekkonid sacculus as compared with the expansion of the scincid sacculus.

f. The papilla basilaris is as long as that of gekkonids, but in contrast to the gekkonids it does not always vary directly in length with the size of the species (table 2 and graph 7). The papilla is somewhat fusiform and tapers very gradually. While the superior end is wider, there is a very short fusiform expansion at the inferior tip. It is probably acoustically significant that while the scincid limbic recess is inferior in position and the gekkonid superior, it is the narrowest part of the papilla basilaris in both families that is enclosed by the limbic recess.

While still typically scincid in all characteristics, the cochlear duct of such forms (elongate skinks) as *Acontias meleagris, Brachymeles tridactylus, Brachymeles vermes, Nessia monodactyla, Ophiomorus tridactylus, Rhodona fragilis, Typhlosaurus cregoi,* and the lygosomids I have examined, show reduction of both the limbic and lagenar portions.

Even within genera such as in *Brachymeles* and *Lygosoma* there is variation from little or no reduction, to considerable reduction of both lagenar and limbic features. It appears that reduction or degeneration of the cochlear duct in skinks is found in those species that are anatomically modified for burrowing.

The cochlear duct, as well as many other anatomical characteristics, appear to be remarkably plastic in the scincid lizards.

14. **Feyliniidae** (plate XIV).

The feylinid cochlear duct is so similar in all details to the scincid duct that it may be included in that general group. In *Feylinia currori* the duct is scincid, but shows a small degree of reduction in size of all its various features (table 2).

15. **Xantusiidae** (plate XV).

a. The xantusiid cochlear duct is undoubtedly scincid in type, but differs sufficiently to clearly differentiate it from the Scincidae and Feyliniidae. The duct is generally more elongate, there is no tendency to bending, and the superior pole of the duct is more attenuated. The limbic area is greater than the lagenar, and the latter largely occupies the anteroinferior portion of the duct.

b. The macula lagenae is somewhat shorter than the papilla basilaris and a good portion of it is set at almost a right angle to the papilla basilaris. The duct length varies with species size.

c. The limbus is thickened and is similar to that of the scincid, but the hillock or swelling on the lateral neural limbic face is inclined at an angle to the papilla basilaris; the limbic swelling is closer to the papilla at the superior end than it is inferiorly. In other words, the neural limbic bulge inclines dorsally more rapidly than the papilla basilaris does.

d. The groove for the perilymphatic duct is moderate in depth and the opening for the perilymphatic sac on the medial face of the limbus is superior in position and relatively larger than that of the scincids.

e. The inferior 30 to 40 per cent of the basilar membrane is enclosed housing an inferior recess. The inferior limbic recess of scincids extends over nearly 60 per cent of the membrane length.

f. The papilla basilaris is elongate, slightly fusiform, and often has a small separate fusiform expansion at the inferior extremity. An inferior fusiform expansion is often observed in the scincids, but is never separated from the main papilla. Both the length and area of the papilla basilaris vary directly with species size (table 2). Except for size differences, the cochlear ducts of *Klauberina*, *Lepidophyma*, and *Xantusia* are very similar.

16. **Cordylidae** (plate XVI).

The cochlear ducts of *Gerrhosaurus* and *Cordylus* are nearly identical.

a. The cochlear duct is fairly elongate and both the lagenar and limbic portions are well developed.

b. The macula lagenae is approximately equal to the papilla basilaris in length, and, I would judge, is relatively less reduced than the scincid lagena.

c. The limbus is elongate and probably has expanded in an inferior direction, but not to the degree that occurred in scincid development. The neural limbus is thick (but not as anteriorly extended as the scincid) and has an incipient projection on its lateral face. Thus, the limbic "lip" is more pronounced than the scincid, but less developed than that of the anguid.

d. The groove for the perilymphatic duct is moderate in depth, and not as superiorly placed as the scincid.

e. As in the skinks and xantusiids, the perilymphatic duct approaches the medial limbic hiatus superiorly, but unlike these types that have long inferior limbic recesses, the medial aspect of the basilar membrane of the cordylids is open. Only short, inferior, and superior limbic recesses are present.

f. The papilla basilaris is long. The papilla gradually tapers from the superior to the inferior end and terminates in a fusiform swelling, but is not divided. The length, and to some degree the area, of the papilla basilaris varies directly with species size (table 2).

17. **Dibamidae** (plate XVII).

a. The cochlear duct of *Dibamus argenteus* is somewhat elongate. The anterosuperior surface of the duct appears to be fused to the inferior saccular wall. While a small constriction separates the lagenar and limbic portions of the duct, these areas are not as clearly separated as in the snakes and in *Sphenodon*. The limbic area is greater than the lagenar.

b. The pars lagena and the macula lagenae appear to be reduced in size and, in my opinion, were derived from a once larger and more extensive area. The macula lagenae is but a short strip at the blunt end of the cochlear duct.

c. The limbus is a thin circular plate with a relatively large centrally located ovoid hiatus.

d. and e. The perilymphatic duct occupies a shallow groove on the medial side of the duct and the medial face of the basilar membrane is mostly open. A short limbic recess is located at each end of the basilar membrane.

f. The papilla basilaris is small (table 2) and oval in shape.

18. **Amphisbaenidae** (plate XVIII).

a. The cochlear duct is somewhat elongate and only superfically divided by a slight constriction between the pars lagenae and the limbic portion. There is a tendency for increase in cochlear duct size with increase in species size, although this relationship is difficult to demonstrate in elongated animals (table 2). The cochlear duct of *Blanus* is much reduced.

b. The pars lagenae appears much reduced in size and is represented by the short, blunt inferior extremity of the cochlear duct. The macula lagenae is a short strip located at the blunt inferior extremity of the duct; its long axis is inclined nearly 90 degrees to the papilla basilaris.

c. The limbus is a thin, almost circular, concave plate with a moderate-sized, central, oval-shaped hiatus. The anterior edge of the neural limbus projects laterally forming an overhanging lip.

d. and e. The perilymphatic duct slightly grooves the medial aspect of the cochlear duct and opens into a largely unenclosed sac over the medial face of the basilar membrane. As in *Dibamus*, short inferior and superior limbic recesses are present.

f. The papilla basilaris is small and ovoid (table 2).

The cochlear ducts of *Amphisbaena fuliginosa, Bipes biporus,* and *Diplometopon zarudnyi* are fairly similar. *Rhinuera floridana* differs from those species in that the lagena is somewhat constricted from the limbic area, and the neural limbic lip, instead of being more anteriorly placed, is represented by a bar-like thickening of the entire neural limbus.

Graph 8 (p. 289) is a summary representation showing the range in length of the papilla basilaris in different lizard families.

Plates XXII and XXIII show in summary form, the anatomical relationships of the cochlear ducts in different lizard families.

Discussion

A detailed study of the lizard cochlear duct has two outstanding values. First, the remarkable diversity of structures probably concerned with auditory phenomena may be studied physiologically and hopefully extend our knowledge concerning hearing mechanisms. Second, the relative diversity of cochlear duct anatomy, at least at the familial level of classification, provides us with characters that may contribute to a clarification of some aspects of lacertilian taxonomy and phylogeny.

Relation of the Anatomy of the Cochlear Duct to Acoustical Performance

Anatomical characteristics that may be related to the acoustic capacity of a particular cochlear duct are the following:

1. *The overall size and configuration of the cochlear duct.* The cochlear duct may be square, triangular, or elongated. Usually the increase in size of the duct is associated with increase in size of the limbus and papilla basilaris, but the total configuration depends on the degree of development of both the lagenar and limbic portions of the duct. While the length of the cochlear duct is directly correlated with the length of the papilla basilaris in birds and mammals, this is not always the case in lizards where the length of the cochlear duct and the papilla basilaris may be independent variables (table 2 and graphs 2–7). However, as is the case in birds and mammals (Schwartzkopff, 1963a), the length of the cochlear duct of lizards usually increases with body size. The absolute length of the cochlear duct is generally greatest in mammals, intermediate in birds, and shortest in reptiles.

While hearing capacity may be related more to papilla basilaris length than cochlear duct length, the factor of overall size and shape of the cochlear duct must be considered in acoustic evaluation.

2. *The relative size of the lagenar portion of the cochlear duct.* A cochlear duct may be relatively large, not because of elongation of the papilla basilaris, but rather because of the shape and length of the macula lagenae. Whether the macula lagenae plays a role in acoustic reception is not known. Afferent nerve fibers from the macula lagenae join nerve fibers from the papilla basilaris, and, according to Hamilton (1963), terminate on small cells in the acoustic area of the brain stem. A similar situation apparently obtains in birds (Schwartzkopff, 1963b). The fact that the macula lagenae is covered by an otolithic membrane would not lead one to suspect that it is an auditory receptor. However, we know that in certain fishes the otolithic membrane-covered macula of the sacculus or utriculus may subserve auditory functions (de Burlet, 1934). Flock (1964), on the other hand, states that Lowenstein has demonstrated that the peripheral (and possibly auditory) portions of these sensory areas in fishes may remain uncovered by the otolithic membrane.

While the possible role of the macula lagenae in auditory reception in reptiles remains to be determined, the size and configuration of the pars lagenae and particularly the macula lagenae certainly affect acoustic reception. In Evans' (1936) study of the cochlear–lagena ratio, he attempted to determine what proportion of the entire cochlear duct was occupied by the macula lagenae and what by the papilla basilaris. Neither from Evans' data, nor from the figures of Retzius (1884) can one determine these values. These values can be obtained only by reconstruction of the entire duct or by gross anatomical study (see p. 271).

3. *The shape and size of the limbus.* The limbus varies in shape from a thin saucer-like plate to a thick elongated structure. Thin platelike limbi are usually associated with small ovoid papillae basilares, and the large limbi with longer and better developed papillae.

4. *The development of a lateral projection or lip from the neural limbus.*

This structure is somewhat variable within lizard families, but on the whole, characteristically different from family to family. The possible significance of the limbic prominence or lip is that it alters the manner in which the tectorial membrane is related to the hair cells of the papilla basilaris, and the extent to which endolymph is enclosed between the tectorial membrane and the neural limbus.

While the great majority of lizards possess a tectorial membrane, it is very odd that some skinks, and possibly other scincomorphic lizards may have lost the tectorial membrane. This feature demands further and very careful study, both to determine if and in what species the tectorial membrane is absent, and to assess the functional significance of this phenomenon. Histological and ultrastructural studies of the relationship of hair cells to the tectorial membrane should reveal further adaptations of acoustical significance.

5. *The size and shape of the papilla basilaris.* The papilla varies from small ovoid aggregates of sustentacular and hair cells, to elongated, fusiform, or divided structures. It is probable that differing auditory capacities, either in pitch or intensity discrimination (Schwartzkopff, 1963a) are related at least in part to the size, shape, and structure of the papilla basilaris.

Graph 8 and table 3 summarize variations in the length and areas of the papilla basilaris in representatives of different lizard families.

6. *The basilar membrane.* This structure varies both in size and shape and usually corresponds to the size and extent of the papilla basilaris, but may vary in extent independently of the degree of development of the papilla basilaris.

7. *The papillar bar.* Underlying the supporting cells of the papilla basilaris is a variously thick bar of modified connective tissue identical to that of the limbus. This bar lends rigidity and support to the overlying supporting and sensory cells of the papilla. This structure may serve to dampen sound waves in acoustic reception. The only previous mention of this structure I have seen, occurs in figure 16 (f), table VIII of Retzius (1884), where he illustrates a "Firste" (bar or ridge) underlying the papilla basilaris of *Lacerta ocellata.*

8. *The development of limbic recesses.* In some types of cochlear ducts the entire medial face of the basilar membrane is not enclosed by any portion of the limbus. In others, various parts of the basilar membrane are enclosed by the limbus. Projecting into the limbic recesses are extensions of the perilymphatic sac. Such enclosed portions of the perilymphatic sac (perilymphatic diverticuli or accessory scalae tympani) which are conducting sound-pressure waves to the basilar membrane may act to intensify or concentrate acoustic energy; thus these portions may play an important part in auditory reception.

It is also possible that sound energy may be transmitted directly across the cochlear duct, rather than all the energy being carried by the perilymphatic duct to the basilar membrane (see discussion in Baird, 1960a).

9. *The number of hair cells*, the innervation of the hair cells, the number of

cochlear ganglion cells, the number of connections of the cochlear nuclei cells, as well as the role of mid- and forebrain centers are certainly all related to hearing capacity but are as yet unstudied in reptiles.

Table 4 summarizes some anatomical differences in the cochlear duct that may be related to the acoustical capacity in different lizard families.

To date, most of our information concerning the acoustical capacities of reptilian cochlear ducts have been derived from studies of cochlear potentials in the laboratory of E. G. Wever and his associates. Table 5 summarizes some of the data derived from these studies.

While both the number of species as well as the number of individual animals so far studied is relatively small, it appears that the iguanids and lacertids are intermediate to relatively poor in their acoustical responses. The anguids, while sensitive at low ranges of pitch, are not very sensitive about 1,000 cps. and the teiids and gekkonids, of all lizards so far examined, are the best performers.

This information correlates well with the anatomical information presented in tables 2, 4, and 5 where it can be seen that the iguanids and lacertids (poor to intermediate performers) have relatively short papillae basilares as well as small papillary areas. It is particularly significant that while but a single specimen of *Anolis carolinensis* was studied by Wever and others (1963a) it gave a better performance than other iguanids. This correlates well with the fact that among the iguanids, the papilla basilaris of the anolids is both longer and greater in area (table 2).

As might be expected, a teiid (*Cnemidophorus tessalatus*) was a better performer than the above types, and members of the Gekkota were very good. Both the teiids and Gekkota have papillae of fair length and area. It is interesting that *Gecko gecko* whose papilla basilaris is twice the length and triple the area of *Coleonyx variegatus* performed less well than the latter species.

Certainly many factors other than papilla basilaris length and areas are important in determining auditory capacity, and further anatomical and neurophysiological studies of lizard cochleae should be of great value.

For the present, one might conjecture that on the basis of anatomical development, at least four categories of relative hearing capacity might be expected among different lizard families. These are:

A. Relatively poor, undeveloped, or regressed.

Chamaeleonid
Anniellid
Xenosaurid
Dibamid
Amphisbaenid

B. Fair.

Iguanid

Agamid
Lacertid

C. Moderately well to good.

Anguid
Anolid iguanians

D. Good to very good.

Teiid
Gekkotid
Pygopodid
Varanid
Scincid
Xantusiid
Cordylid

An artificial division such as this presupposes that the length and area of the papilla basilaris, the type of limbic lip and disposition of the tectorial membrane, and the development of limbic recesses are related to hearing capacity. Other factors of importance are the variations in middle ear anatomy, the detailed structure of the papilla basilaris, and the central nuclei and their connections.

The only lizards known to have developed vocality and auditory communication are geckos (Evans, 1936); thus, it is not surprising that this group has an "advanced" type of cochlear duct.

Since other lizards with seemingly advanced types of cochlear ducts (teiids, scincids, xantusiids, cordylids, and varanids) apparently have not developed a voice, it seems likely that they use their hearing ability for defensive or foraging activities. One might imagine that a skink resting in an underground burrow, or a xantusiid hidden between the leaves of a rotting Joshua tree log, are easily capable of perceiving the sounds made by insect or termite activity in their immediate vicinity.

Beach (1944), in a discussion of hearing in reptiles, cites three studies relative to lizards. Kuroda (1923) found modifications of certain visual reflexes in *Tachydromus tachydromoides* in response to stimulus with a bell or Galton whistle. Beatty (1932) working with *Lacerta viridis,* observed responses to auditory stimuli, and Berger (1924), with *Lacerta agilis* and *Lacerta vivipara,* found that specific eye reflexes, a modified respiratory rhythm, and trained learned responses could be induced by loud noises as well as tonal stimuli.

Evans (1936) also comments on an extremely interesting and significant observation of G. M. Allen who described a case of vocal expression in the skink, *Mabuya bensonii*, the sounds being a series of bark-like staccato noises.

It is well known that alligators are vocal (Beach, 1944), and possess a better developed cochlear duct than lizards; the duct is longer, partially twisted, and

Table 4. *Some anatomical differences in the cochlear duct that may be related to the acoustical capacity in different families of lizards.*

Family	Macula lagenae	Limbus	Lateral–neural limbic modification	Papilla basilaris	Limbic recesses
I Iguanidae	Large, long, 2 to 3 times length of papilla basilaris	Small to moderate in size	Thickened bar	Relatively short, but elongate	Very short inferior and superior recesses
II Agamidae	"	"	Thickened bar; slightly better developed inferiorly	"	"
III Chamaeleonidae	Moderate	Reduced to thin saucer-like plate	None	Small circular to ovoid in shape	None
IV Anguidae	Moderate, 2 to 3 times length of papilla basilaris	Moderate, ovoid, large basilar membrane	Somewhat prominent, elongate, sharply undercut bar	Short to moderate, slightly fusiform, elongate	Very short superior and inferior recesses
V Anniellidae	Reduced	Reduced to thin saucer-like plate	Anterior edge forming bar-like projection	Small, ovoid	None
VI Xenosauridae	Moderate	"	None	Small, ovoid	None
VII Helodermatidae	Moderate	Moderate, thick	Rounded prominence	Moderate, elongate	Short superior recess
VIII Varanidae	Moderate	Large, elongate, sometimes divided hiatus	Thickened neural ridge	Elongate, sometimes divided (longer superior portion)	Relatively long superior and short inferior recesses
IX Lacertidae	Moderate to relatively large	Moderate, ovate, divided hiatus	Prominent, fairly thick ridge projecting from anterosuperior middle part of neural limbus	Elongate, divided; two portions approximately equal in length	Very short superior and inferior recesses
X Teiidae	Large	Large, elongate	Prominent, thick process projecting from mid 50–60% of limbus	Moderate to elongate, slightly fusiform	None

TABLE 4. *Continued.*

FAMILY	MACULA LAGENAE	LIMBUS	LATERAL-NEURAL LIMBIC MODIFICATION	PAPILLA BASILARIS	LIMBIC RECESSES
XI Gekkota	Large	Large, ovate to elongate	Thin, extensive awning-like process extending over papilla basilaris	Elongate, slightly fusiform	Long superior recess ($\frac{2}{3}$ basilar membrane recessed)
XII Pygopodidae	Moderately large	"	"	"	Long superior recess ($\frac{3}{4}$ basilar membrane recessed)
XIII Scincidae	Moderate, except in some reduced species	Large, shows lateral curvature	Ridge-shaped thickening	Elongate, slightly fusiform	Long inferior recess ($\frac{3}{5}$ basilar membrane recessed)
XIV Feyliniidae	Moderate, though reduced	Reduced scincid	Ridge-shaped thickening	Similar, but slightly shorter and thicker than scincid	Long inferior recess ($\frac{3}{5}$ basilar memberane recessed)
XV Xantusiidae	Moderate	Relatively large, elongate	Ridge-shaped thickening	Elongate, slightly fusiform	Long inferior recess ($\frac{3}{10}$ to $\frac{2}{5}$ basilar membrane recessed)
XVI Cordylidae	Moderate	Moderately large, elongate	Slightly projecting ridgelike thickening	Elongate, slightly fusiform	Short inferior and superior recesses
XVII Dibamidae	Relatively short	Thin, saucer-like plate	Very small lip	Small, ovoid	Shallow and short recesses
XVIII Amphisbaenidae	Relatively short	Thin, saucer-like plate	Anterior edge forming bar-like lip	Small, ovoid	Shallow and short recesses

Table 5. *Summary of auditory responses in various reptiles obtained by the cochlear potential method.*

Species	*General range (cps)*	*Range of greatest sensitivity (cps)*	*Source*
Crocodilia			
Caiman sclerops	20 to 6,000	100 to 3,000 (very sensitive)	Wever and Vernon, 1957
Chelonia			
Emydidae			
Clemmys insculpta		*Clemmys* very	Wever and Vernon,
Chrysemys picta	up to 3,000	sensitive up to 500	1956
Pseudemys scripta		(sensitivity in range of –40 to –60 db.)	
Ophidia			
Colubridae			
Pituophis m. melanoleucus		100 to 500 (moderate	Wever and Vernon,
Thamnophis s. sirtalis	to 700	sensitivity; –20 db.)	1960
Thamnophis s. sauritus			
Natrix sipedon pictiventris			
Lacertilia			
Iguanidae			
Uma notata	Decreased sensi-	700 to 2,000 (moderate	Wever and Peter-
Sceloporus clarkii	tivity below 700	sensitivity; –20 db.)	son, 1963
Urosaurus ornatus	or above 2,000		
Sauromalus obesus	"	400 to 4,000; peak at 2,500	Wever *et al.*, 1963a
Anolis carolinensis		400 to 3,000 (good sensitivity; –30 db.)	Wever *et al.*, 1963a
Lacertidae			
Eremias velox	1,000 to 3,000	500 to 1,000 (low sensitivity; +35 db.)	Wever *et al.*, 1963a
Anguidae			
Gerrhonotus multicarinatus	Decrease below 1,000 or above 2,000	300 to 500 (very sensitive)	Crowley, 1964
Teiidae			
Cnemidophorus tesselatus	Up to 17,000 to 19,000!	400 to 4,000 (moderate sensitivity)	Wever *et al.*, 1963a
Gekkota			
Gecko gecko	100 to 7,000	200 to 400 (decrease above 3,000)	Wever *et al.*, 1963b
Hemidactylus turcicus	100 to 10,000	(moderate sensitivity)	Wever *et al.*, 1964
Coleonyx variegatus	100 to 10,000	400 to 1,000 (very sensitive)	Wever *et al.*, 1964

in *Alligator mississippiensis* the papilla basilaris is two to five times the length and 10 to 30 times the area of most well developed lizard papillae (table 2).

Bellowing has been reported in certain turtles (Kelemen, 1963) but the cochlear duct of these species has not been studied.

THE RELATION OF COCHLEAR DUCT ANATOMY TO LACERTILIAN CLASSIFICATION

Probably the outstanding feature of the cochlear duct of lizards is that the duct is recognizably distinct in every family of lizards so far studied. And even though the degree of variation is considerable within some families, it is always possible to define the cochlear duct characteristics of any particular family. When the degree of intrafamilial variation is relatively large, the data on differences may be useful in intrafamilial classification. These features will be discussed in detail under family headings.

Shute and Bellairs (1953) were probably the first to recognize the taxonomic significance of the lacertilian cochlear duct, and since then, Baird (1960a), Hamilton (1960, 1964) and Schmidt (1964) have verified this observation. Also, the studies of Hamilton and Baird have shown that detailed analysis of the perilymphatic spaces, and variation in other parts of the membranous labyrinth are all important in the ultimate analysis of lacertilian classification and phylogeny. Wherever useful, all anatomic, physiologic, biochemical, or behavior information should contribute to the solution of taxonomic and phylogenetic relationships.

While the following tentative groupings are based to a large degree on the anatomy of the cochlear duct many relationships are strengthened or basically indicated by the general features of lacertilian classification as set down by Camp (1923), McDowell and Bogert (1954), and Romer (1956).

This scheme does not imply a phylogeny, but groups families according to the anatomical similarities of their cochlear ducts.

I. Iguanidae
   Agamidae
II. Chamaeleonidae
III. a. Anguidae
   b. Anniellidae
   c. Xenosauridae
   d. Helodermatidae
IV. Varanidae
V. Lacertidae
   Teiidae
VI. Gekkota
   Pygopodidae
VII. a. Scincidae
   b. Feyliniidae
   c. Xantusiidae
   d. Cordylidae
VIII. Dibamidae
IX. Amphisbaenidae

I. **Iguanidae**
Agamidae

The cochlear duct of this assemblage, while fairly large, has a relatively small but thickened limbus and does not possess a distinctive limbic lip. The macula lagenae is relatively long and the papilla basilaris, short. The main difference between the ducts of the iguanids and agamids is the exact shape of the duct and the nature of the neural limbic thickening.

The cochlear duct of this group does not have marked specializations of any one feature and may be considered generalized, or unspecialized.

From a study of the cochlear ducts of 49 species representing 29 genera of iguanids, the ducts of the anolids differ from most other iguanids in having a more elongate limbus and a longer papilla basilaris. Both the length and area of the anolid papilla basilaris are approximately double that of other similarly sized nonanolid iguanids. The genus *Tropidurus* has an unusually pointed duct and a high bar-like neural limbic thickening.

The cochlear ducts of the three Old World lizard genera, *Brachylophus*, *Chalarodon*, and *Oplurus*, are characteristically iguanid.

At the present time, I am unable to relate the structure of the iguanid–agamid cochlear duct to that of any other assemblage.

II. **Chamaeleonidae**

The cochlear duct of the true chamaeleons shows no separation of lagenar and limbic portions, is triangular in shape, and the outstanding features, a thin platelike limbus and a small circular papilla basilaris. While the duct is characteristic for this family, it is not sufficiently similar to that of any other group to indicate a clear-cut relationship.

Unlike the interpretations of Hamilton (1964) and Schmidt (1964), I believe the chamaeleonid cochlear duct is degenerate and not primitive. A small limbus and papilla basilaris do not necessarily indicate a primitive condition, but may represent a regressed or degenerate state. Similar regressed conditions are seen also in *Anniella* and *Xenosaurus* (see below).

While there is insufficient evidence on the basis of cochlear duct anatomy alone to relate the Chamaeleonidae to the Agamidae, it is entirely conceivable that the chamaeleonid duct could result from regression of the agamid type.

It is particularly interesting that a group (Chamaeleonidae) that has developed visual acuity to a high degree (Walls, 1942, p. 625) should either not have developed or have experienced degeneration of the auditory organ.

III. a. **Anguidae**

The development of a prominent neural limbic thickening probably indicates some advance in cochlear duct construction. However, the papilla basilaris and macula lagenae remain relatively short. The above-mentioned "advance" may correlate with the greater auditory acuity in the lower ranges of pitch discrimination and the short papilla with relatively poor performance in the higher ranges (table 5).

I consider the cochlear duct of anguids more advanced than the iguanid–agamid type, but not as advanced as that found in the teiids, gekkonids, and skinks.

Hamilton (1964) states that the cochlear duct of *Anguis* approaches a primitive state. This is not the case, for the duct of *Anguis fragilis,* while reduced, shows all the characteristics of an anguid lizard.

It is interesting that *Anguis fragilis* and *Ophisaurus ventralis* show reduced features in both the lagenar and limbic portions of the cochlear duct. These species are burrowing forms and like many burrowing skinks and *Anniella* have lost the external ear opening and show degenerative cochlear duct changes.

III. b. **Anniellidae**

The macula lagenae and papilla basilaris both appear to be regressed structures in the cochlear duct of *Anniella pulchra*. Further, the small anteriorly placed limbic lip might represent the remnant of a once larger projection. I believe this is another example of degeneration of the cochlear duct that is associated with the assumption of a burrowing habitus.

While the cochlear duct of *Anniella* does not show close anatomical affinities with any other group, it is conceivable that it could result from the degeneration of an anguid-like structure.

III. c. **Xenosauridae**

The limbic portion of the cochlear duct of *Xenosaurus grandis* is markedly reduced, while the lagenar area remains moderate in proportion. Like *Anniella,* the duct of *Xenosaurus* is very different and I find no definite clues to suggest its taxonomic relationship.

It is conceivable that the duct of *Xenosaurus* could be derived from either iguanid or anguid stock; because of other anatomical features (Camp, 1923; Romer, 1956), however, I include it among the anguinomorphs.

III. d. **Helodermatidae**

The limbus of *Heloderma* is heavier and the neural limbic thickening better developed than that of the iguanids, but not as well developed as that of the anguids. The papilla basilaris is longer than either the iguanid or anguid. While the helodermid duct could have been derived from either the iguanid or anguid type, on the basis of other anatomical features (Romer, 1956), I tentatively include it in the anguid group.

IV. **Varanidae**

The cochlear duct of the varanids is moderately advanced; the duct is large and elongate, the papilla basilaris is long and frequently divided, and a moderately long limbic recess is present.

While the lacertids are the only group having a clearly divided papilla basilaris, the varanids show a variable tendency in this direction, and the teiids and scincids show what I interpret as remnants of such a condition. For the present, the significance of a divided papilla basilaris is not clear.

It is interesting that the nerve to the papilla basilaris in *Heloderma* is bifid, while the papilla is not divided. However, the much thickened neural limbus of *Heloderma* is reminiscent of that of *Varanus*. Thus, as in certain other anatomical characters (McDowell and Bogert, 1954) the helodermids, varanids, and anguids are probably related.

V. Lacertidae
Teiidae

The cochlear duct of these two families, while distinctive for each, show definite similarities. This is to be expected in two families that share many common anatomical attributes.

The cochlear duct of the teiids is generally larger and the limbus and papilla basilaris longer than that of the lacertids. While the papilla is not divided in the teiids as it is in the lacertids, a constriction near the superior end in the teiids indicates that it may have been divided at an earlier state of development.

The limbic lip while slightly different in each of these two families is generally similar in appearance. Neither family has developed a limbic recess of significant size.

As far as the anatomy of the cochlear duct is concerned, the lacertid–teiid complex cannot be associated clearly with any other group of lizards.

VI. Gekkota (including **Gekkonidae, Eublepharidae, Sphaerodactylidae, Uroplatidae**)
Pygopodidae

While I have studied the cochlear duct of 19 genera of gekkonids, I have seen but two genera of Eublepharids (*Coleonyx* and *Eublepharis*) and two genera of sphaerodactylids (*Gonatodes* and *Sphaerodactylus*). I have also seen *Uroplatus* and three genera of pygopodids.

The gekkonid duct seems to be remarkably stable, and except for increase in the length of the cochlear duct, limbus, and papilla basilaris in relation to body size, the anatomical details are remarkably constant throughout this group. On the basis of cochlear duct anatomy alone, the Gekkota comprise a uniform group.

Hamilton (1960) in his studies on the morphology of the inner ear of certain gekkonid lizards which takes into account other structures than the cochlear duct, concludes that there are more fundamental differences within this assemblage than I could find. Until more genera and species are studied, and more quantitative comparisons are made, further discussion at this time would not seem fruitful.

The pygopodid cochlear duct is remarkably similar to the gekkonid. The main differentiating feature seems to be the angle of inclination of the macula lagenae to the papilla basilaris. While I have seen the ducts of only three pygopodid genera, these are anatomically very similar and differ mainly in size relationships. The cochlear duct of *Aprasia pulchella* is somewhat reduced in size, and is essentially a miniaturized replica of an advanced pygopodid duct.

On the basis of the marked development of the limbic lip, the increase in length and area of the papilla basilaris, and the development of a long superior limbic recess, the gekkonids and pygopodids in relation to other lizards have an advanced type of cochlear duct. These are not the only advanced types of cochlear ducts among the lizards, however, inasmuch as the scincids and xantusiids have evolved advanced types too that are somewhat different in anatomical details (see below).

It is interesting that a group (gekkonids) that displays many so-called primitive anatomical features, should have evolved a fairly advanced cochlear apparatus.

Hamilton (1964) has noted also that the development of the gekkonid duct was posterosuperiorly and at the expense of the sacculus, whereas the lengthening of the scincid duct was anteroinferiorly and not at the expense of the sacculus.

At the present, I am unable to relate the cochlear duct of the gekkonid–pygopodid complex to that of any other living group.

VII. a. Scincidae

The scincid cochlear duct is an advanced structure that is narrowed, elongated, slightly curved (incipient coiling?), and has a relatively long, slightly fusiform papilla basilaris, and an extensive inferiorly directed limbic recess. The lateral neural limbic wall, while having a thickened ridge, does not develop a lip as do the lacertids, teiids, gekkonids, and pygopodids. Retzius (1884, p. 100) is of the opinion that the scincid cochlear duct is the most highly developed type found in the saurians and represents an important transitional stage from the lizard to the crocodilian type.

Whether the lack of a limbic lip affects the auditory capacity of the scincids is unknown as these forms have not been studied acoustically. While other factors may be of much greater importance, the crocodiles and birds, like the scincids, do not possess a limbic lip, and apparently achieve greater auditory powers by means of an increase in the length and area of the papilla basilaris.

Study of graph 7 shows that there is a great range of cochlear duct and papilla basilaris length in the skinks. This variability correlates with certain anatomical changes that are related to the variety of life modes that are found in the skinks. For the present it appears that in species of skinks modified for burrowing, and where there have been changes in the external ear, the cochlear duct shows degenerative changes.

While an extensive analysis of correlative changes in the scincid cochlear duct will be undertaken in a future paper, it is noteworthy that even with a considerable degree of anatomical change, such as occurs in *Acontias,* some species of *Brachymeles, Nessia, Rhodona,* the lygosomids and the typhlosaurids, the cochlear duct, while also showing reduced features, is always recognizably scincid. No family of lizards has what we may without doubt interpret as a "primitive" cochlear duct; regression or reduction of the duct has in fact occurred and might mislead one to believe that an evolutionary primitive structure is present. Application of the term "primitive" to an obviously degenerate state is a contradiction in fundamental meaning.

VII. b. Feyliniidae

The cochlear duct of *Feylinia currori,* while reduced in many features, is undoubtedly scincid.

VII. c. Xantusiidae

In most regards, the cochlear duct of the xantusiids is very similar to that of the scincids. The differences in the neural limbic ridge, the limbic recess, the shorter macula lagenae, together with other anatomical features indicate the separate familial status of the xantusiids, but suffice to show the close affinities of this group to the scincids. The differences between the cochlear ducts of *Klauberina, Lepidophyma,* and *Xantusia* are related mainly to the size of the animal and not to any structural differences in the ducts.

VII. d. Cordylidae

The relationship of the cordylids to the scincoid lizards is not as easy to demonstrate as is that of the scincids and xantusiids to one another. The cochlear duct is not as elongated as the scincid, and while the neural limbic ridge is better developed in the cordylids, there is little closure of the medial aspect of the basilar membrane. The sacculus of the cordylids is also not as large as that of the scincids indicating a lesser degree of ventral expansion.

The relatively long papilla basilaris and the lack of a definite limbic lip, together with other anatomical characteristics (Romer, 1956) would indicate a scincid relationship of the cordylids.

VIII. Dibamidae

The cochlear duct of *Dibamus argenteus* is probably a degenerate structure and while it superficially resembles the duct of the amphisbaenids one cannot say that these two groups are related to one another, or to any other group, on the basis of cochlear duct anatomy alone.

IX. Amphisbaenidae

It is difficult to be certain whether the cochlear duct of the amphisbaenids is degenerate or specialized. It certainly is not primitive.

The limbus is a thin saucer-like plate, similar to that of the chamaeleonids, *Anniella*, or *Xenosaurus* in which the cochlear duct is probably regressed or degenerate. The lagenar portion of the duct in the amphisbaenids seems to be more obviously degenerate. If this is the case, then, it is highly likely that the limbic portion has also been reduced from some better developed precursor. While the cochlear duct may have arisen by reduction of a once more fully developed type, it might be considered that the auditory apparatus is a specialized one representing an adaptation to a burrowing habit. Camp (1923) is of the opinion that the outer ear of amphisbaenids is not a degenerate structure, but a highly specialized one.

The fact that the lagenar and limbic portions of the duct are well joined speaks somewhat against ophidian relationship, but further studies in this direction are certainly indicated as *Typhlops* has a cochlear duct somewhat similar to that of the amphisbaenids (unpublished observations). Baird (1960b) concludes that the auditory apparatus found in typhlopid snakes is a specialized adaptation for burrowing.

It may well be that the amphisbaenids are not lacertilians and either belong to another or a separate order.

The cochlear ducts of anelytropsids, shinosaurids, or *Lanthanotus* have not been studied.

Summary

The gross morphology of the cochlear duct of 205 species, representing 131 genera and 18 families of lizards was studied. While the cochlear duct differs considerably in its morphology from one family to another, it is sufficiently stable at the family level of classification to be diagnostically characteristic for any one family. The degree of intrafamilial variation is different from one family to another. Morphological variations occur in the shape and size of the entire duct, and in the relative sizes of the lagenar and limbic portions of the duct. The limbus undergoes modifications of both surfaces, forming thickenings, projections, or lips on its lateral face, and recesses on the medial aspect. The macula lagenae varies greatly in length and area. The papilla basilaris may be short, elongate, circular, ovoid, fusiform, entire, or divided, and varies in total length and area. In most lizard families the size of the cochlear duct and limbus, and the length and area of the papilla basilaris varies directly with species size; in others, correlation between size of duct elements and species size is not as marked.

The auditory capacity of a particular cochlear duct is probably related to many of the above anatomical differences. These are discussed in relation to acoustical studies that have been made on reptilian cochleae.

The morphological features of the cochlear duct in certain families is indicative of close taxonomic relationships. The most clear-cut anatomical

similarities between the cochlear ducts of different groups are exemplified in the iguanid–agamid, lacertid–teiid, gekkonid–pygopodid, and scincid–xantusiid associations.

In other families, cochlear duct morphology in itself, is not greatly helpful in revealing interfamilial taxonomic relationships.

Various elements of the cochlear duct may undergo regressive changes in species of some families. In no case, however, does regression or degeneration progress to the degree that the familial status of a particular cochlear duct is in doubt. In some very small species, miniaturization of the duct may occur.

Both interfamilial and intrafamilial relationships of the cochlear duct are discussed.

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NOTE CONCERNING THE VIEWING OF BLACK-AND-WHITE STEREOPHOTOGRAPHS

An understanding of the anatomical details of the lizard cochlear duct is best achieved by three-dimensional visualization of the intact structure. To accomplish this stereophotographs of the cochlear duct are presented.

While stereocolor transparencies are superior to black-and-white stereophotographs, their cost of publication is high, and for the time being black-and-white stereophotographs are presented.

The use of black-and-white stereophotographs was common in the latter part of the nineteenth and early part of the twentieth centuries, but is used much less often today.

de Burlet (1934) very effectively illustrated his excellent articles on the ear of vertebrates with stereo black-and-white photographs.

Since color transparency stereo pairs are easily viewed in readily available special viewers, difficulty in achieving a full three-dimensional effect is rarely experienced. The viewing of black-and-white stereophotographs, on the other hand, is more difficult and requires some special practice or the acquisition of a stereoscopic viewing device.

Judge (1926, pp. 78–79), in a discussion on the viewing of stereograms, states: "It is possible to experience stereoscopic, *i.e.*, relief and perspective, effects without the aid of the camera, or stereoscope, as will be appreciated from the following simple test.

"Draw two circles or black dots about ¼ inch diameter at a horizontal distance apart of about 2 inches; it will render the test easier if these are drawn near the top edge of a sheet of white paper. If the eyes be focused on these dots in the ordinary way, both will be seen distinctly, but if the paper be held at about 15 to 18 inches from the eyes, and the dots be observed with the eyes accommodated for a long range, or infinity, they will be found to merge into a single central dot; in most cases there is also a fainter or ghost image on each side. It is better to hold the paper in front of the eyes at the distance mentioned and whilst still looking at a distant object to slowly move the paper upwards, and without altering the position of the eyes to look at the dots; they will appear to travel inwards and to merge.

"Some persons are able to merge objects in this way without difficulty, and can view stereoscopic prints without the aid of a stereoscope. It is also possible by 'crossing' the eyes, or squinting, to obtain a stereoscopic effect when viewing a 'pair' of illustrations and without the aid of any viewing apparatus.

"The principle to be observed when viewing stereoscopic prints or illustrations is for the right eye to see only the print taken with the right-hand lens, and the left eye that with the left lens. Both views should appear superposed. Unless the observer is able to merge the views in the manner previously indicated, he will find it impossible to concentrate the attention of each eye on its respective illustration, so that some artificial aid becomes necessary."

One of the simplest methods of viewing a stereogram is that illustrated by Judge in his figure 43 (figure 10) and consists of a vertical black screen S placed in front of the two views A and B of the stereogram, and moved backwards or forwards until it just about occupies the position indicated. It will be

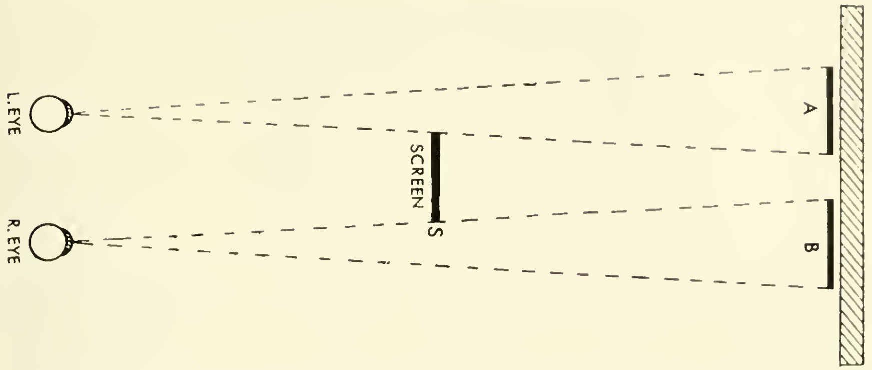

Figure 10. A simple method of viewing stereograms (from Judge, 1926).

evident that the black screen S prevents the right eye from seeing the left view and the left eye from observing the right view. "A convenient way to carry out this method, or rather to practice it, is to place the two reduced width stereoscopic prints against a book on a table and to bend a piece of tin or cardboard in the form of an angle arranged at the required level, near the edge of the table. After a certain amount of practice, the screen S can be dispensed with in many cases."

If one desires, a stereopticon, or stereoscopic viewing device may be purchased.

PLATE I

Family IGUANIDAE

Crotaphytus wislizeni (CAS [14])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 23

Stereopair × 26 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been partly cut away from the lateral face of the duct. The sacculo-cochlear duct lies to the right. The limbus and papilla basilaris are centrally placed. The macula lagenae courses down the anterior (left slope) edge and then onto the medial surface of the duct; this can be seen best in the photographs. A portion of the medial wall of the sacculus is present in the photograph, but not in the drawing.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 23

Stereopair ×26 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The course of the macula lagenae can be visualized better in this view. Note the nerve branches supplying the macula lagenae.

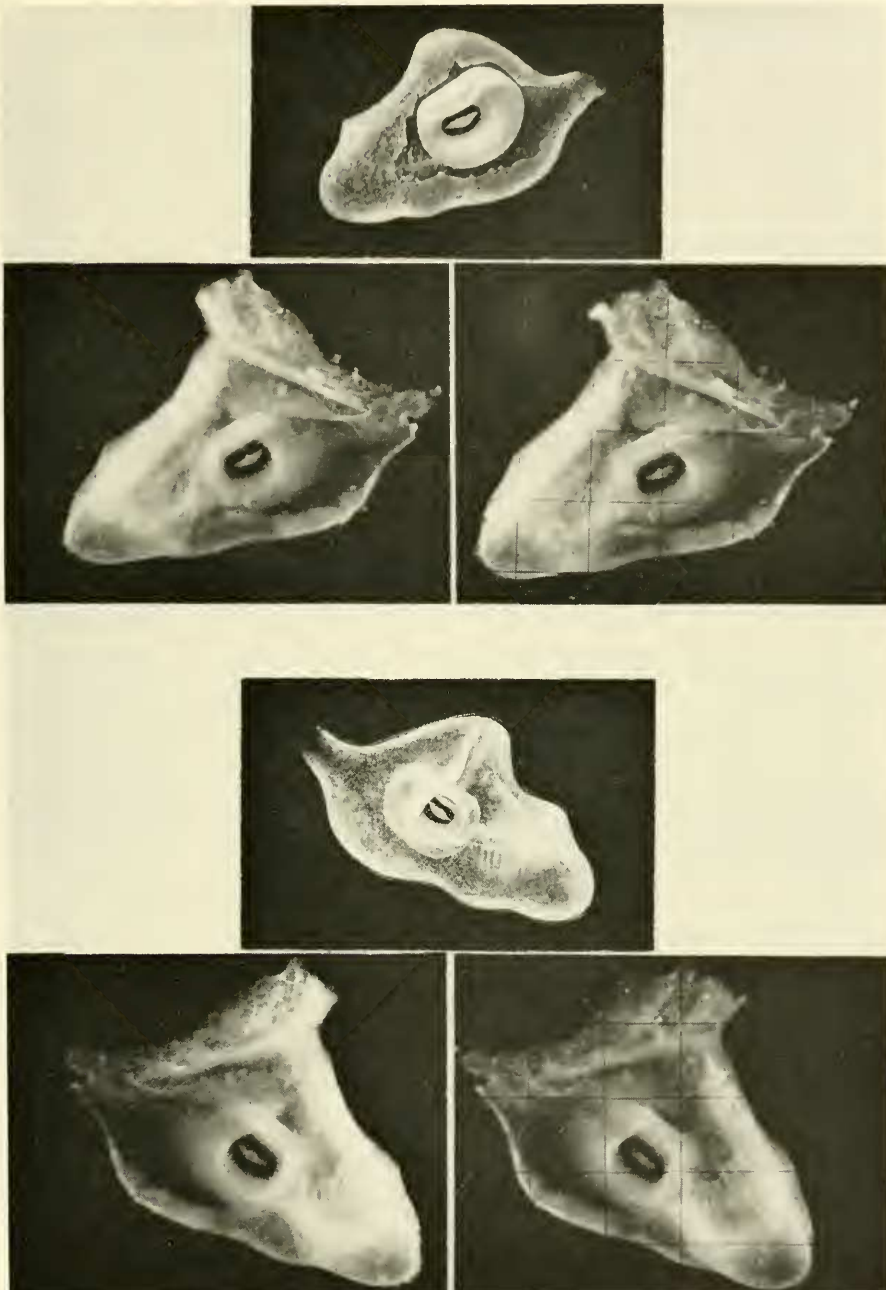

Plate I. The cochlear duct of *Crotaphytus wislizeni* (Iguanidae).

PLATE II

Family AGAMIDAE

Agama agilis (CAS 86343 [25])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 23

Stereopair × 32 (one grid division = 0.25 mm.)

Posterosuperior is to the right, and anteroinferior to the left. Most of the vestibular membrane has been removed. The sacculo-cochlear duct is seen in the drawing, but not in the photograph. The course of the macula lagenae down the anterior (left slope) aspect of the cochlear duct is best seen in the medial view. The bright area in the upper right part of the stereopair is a portion of the macula of the sacculus.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 23

Stereopair × 32 (one grid division = 0.25 mm.)

Posterosuperior to the left, anteroinferior to the right. The macula lagenae passes down the anterior (right slope) of the duct and then curves onto the medial wall. Very short limbic recesses are present. The nerves to the macula lagenae have been torn away just before they supply the length of the macula lagnae.

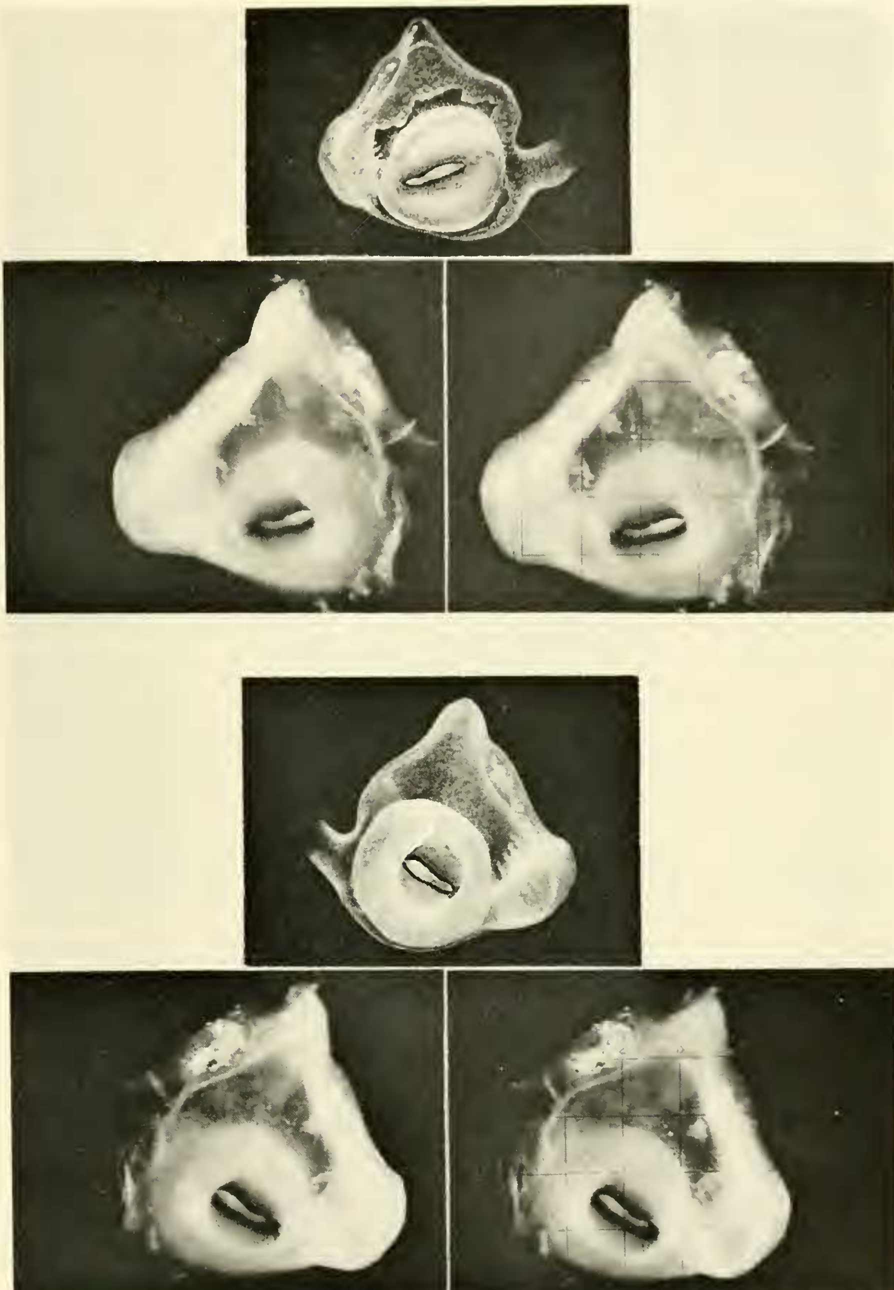

Plate II. The cochlear duct of *Agama agilis* (Agamidae).

PLATE III

Family CHAMAELEONIDAE

Chamaeleo sp. (CAS [311])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 28

Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The sacculus remains attached to the cochlear duct in the photograph, but is not represented in the drawing. The vestibular membrane has not been removed. The thin saucer-like limbus is clearer in the drawing. The nerve to the papilla basilaris is seen in the photograph, but it has not been included in the drawing. The nerve to the papilla basilaris in this specimen is divided into a larger posterior, and a smaller anterior branch. The course of the macula lagenae down the anterior (left) duct wall and then onto the medial wall may be observed in both lateral and medial views.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 28

Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is at the top, and anteroinferior at the bottom. A short superior limbic recess is visible. A small divided nerve supplies the papilla basilaris; multiple nerve branchlets supply the macula lagenae.

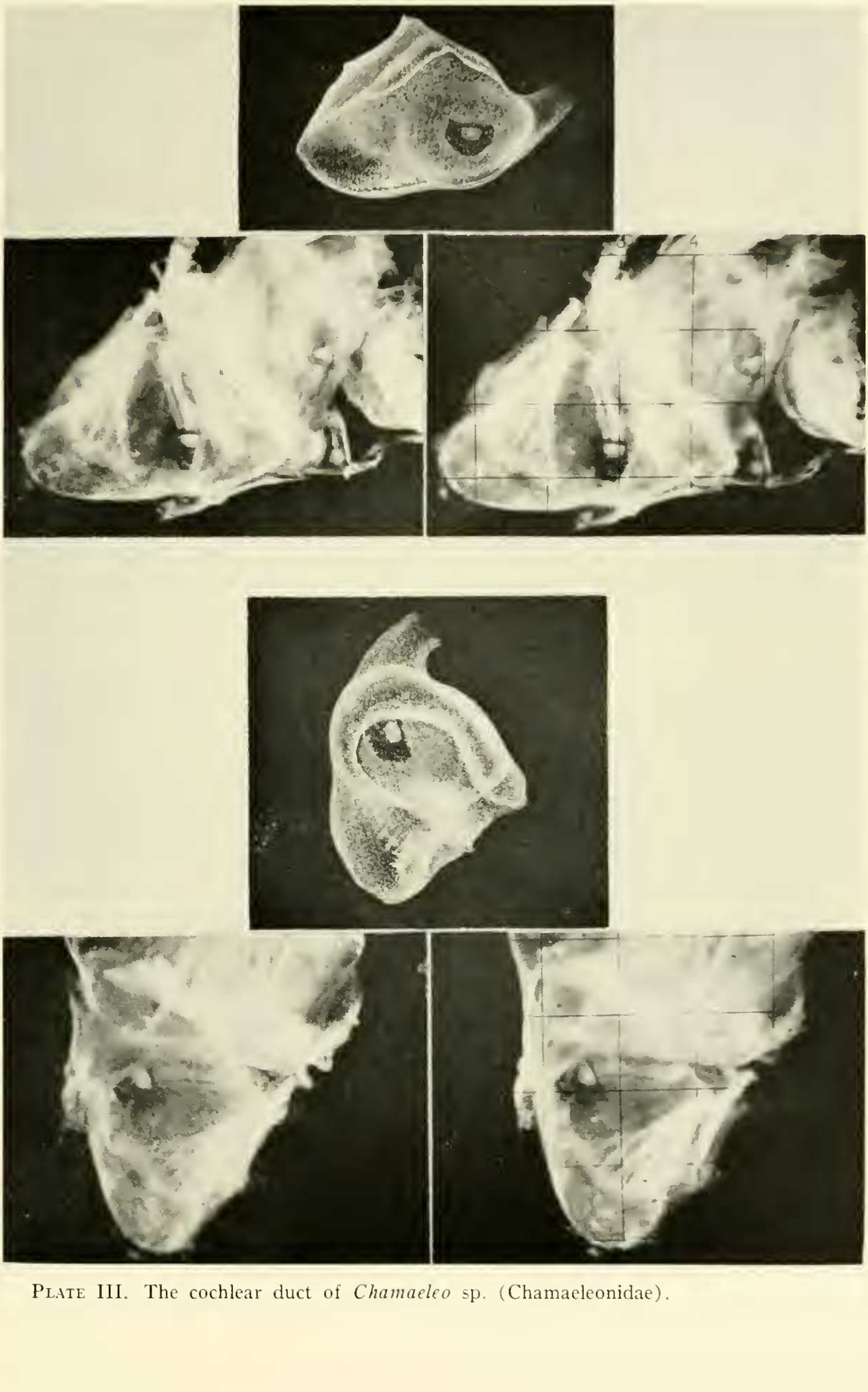

Plate III. The cochlear duct of *Chamaeleo* sp. (Chamaeleonidae).

PLATE IV

Family ANGUIDAE

Diploglossus lessonae (CAS 49540 [61])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 22

Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior is to the left. The vestibular membrane has been partially removed. While the nerves are not depicted in the drawing, three main branches are seen in the photographs. The nerve to the right supplies the crista of the posterior ampulla (cut off). Centrally, behind the neural limbus, is the nerve to the papilla basilaris, and above and to the left is the nerve to the macula lagenae. The macula lagenae is seen on the anterosuperior (upper left) and medial parts of the cochlear duct.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 22

Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior is to the right. The three nerve branches mentioned above are better seen on the photographs of the medial side of the duct. The flanges housing the perilymphatic duct are quite prominent.

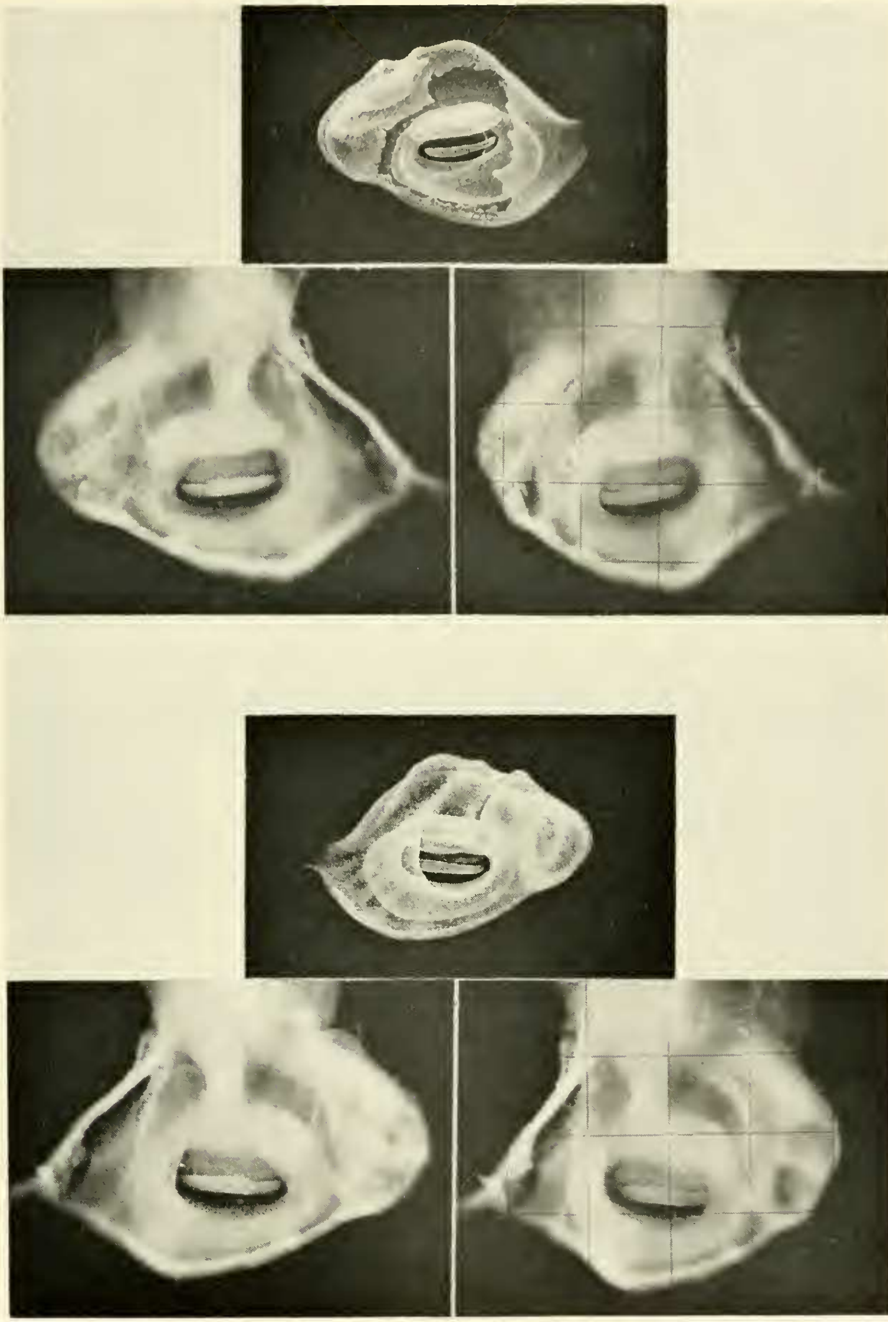

Plate IV. The cochlear duct of *Diploglossus lessonae* (Anguidae).

PLATE V

Family ANNIELLIDAE

Anniella pulchra (CAS 17848 [343])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing ×29

Stereopair × 36 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. In the photograph the nerve to the papilla basilaris courses down the medial side of the neural limbus.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 29

Stereopair ×36 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The lagena lies to the right (anteroinferior) and the opaque white structure within its cavity is the otolithic membrane overlying the macula lagenae. The heavy opaque structure at the top of the photograph is the posterior branch of the auditory nerve, but only the division supplying the papilla basilaris is present.

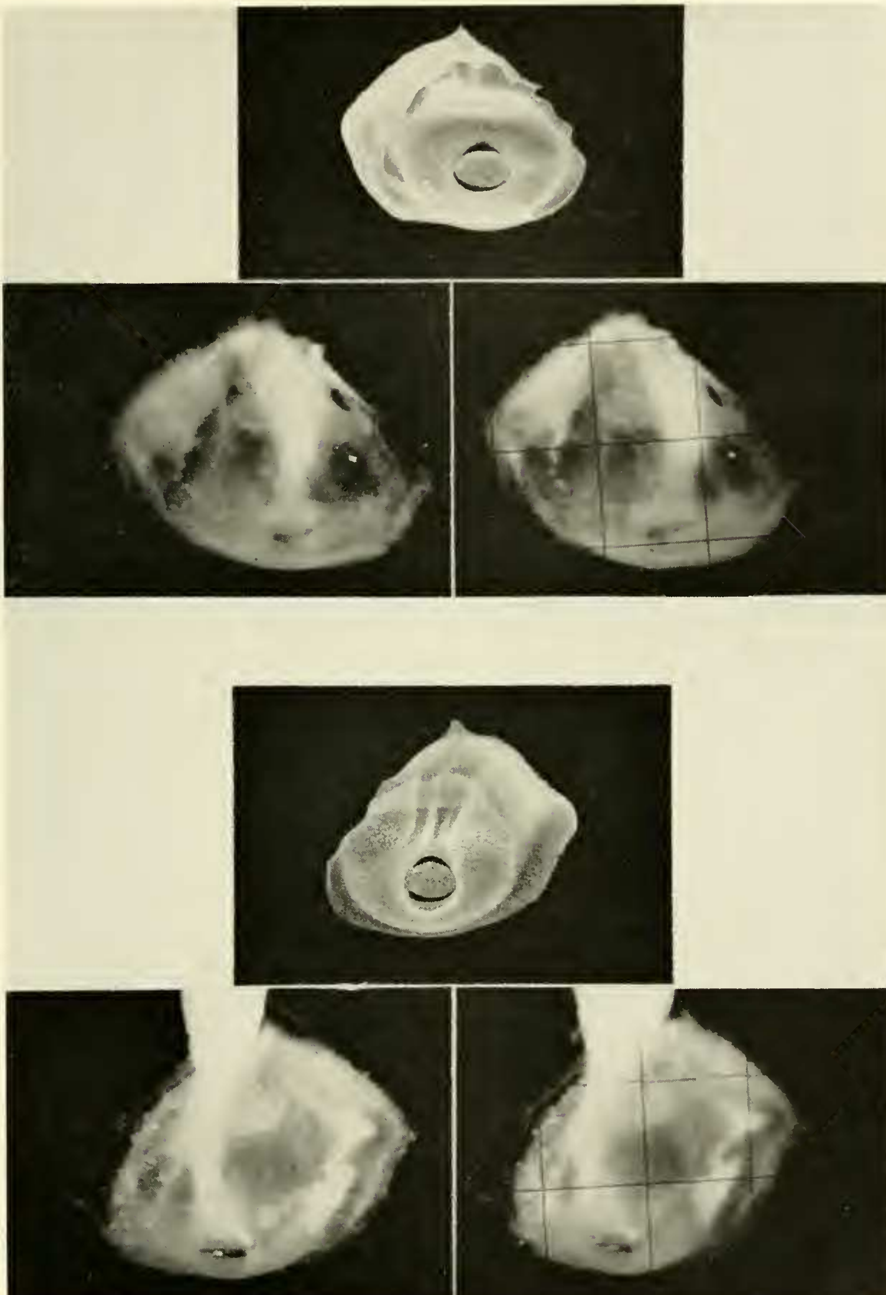

Plate V. The cochlear duct of *Anniella pulchra* (Anniellidae).

PLATE VI

Family XENOSAURIDAE

Xenosaurus grandis (CAS 87839 [344])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 19

Stereopair × 19 (one grid division = 0.58 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane is intact. The opaque white elongate structure on the right edge of the photograph is the nerve to the crista of the posterior ampulla. To the left of this is the long slender nerve to the papilla basilaris. The groove on the upper left corner (anterior edge) of the duct is for the perilymphatic duct. The macula lagenae extends in an arc-like fashion from the anterolateral to the anteromedial portion of the duct.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 19

Stereopair × 19 (one grid division = 0.58 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The nerve branches to the macula lagenae spread out to supply this structure. The nerves to the papilla basilaris and the posterior crista are also quite evident in the photographs.

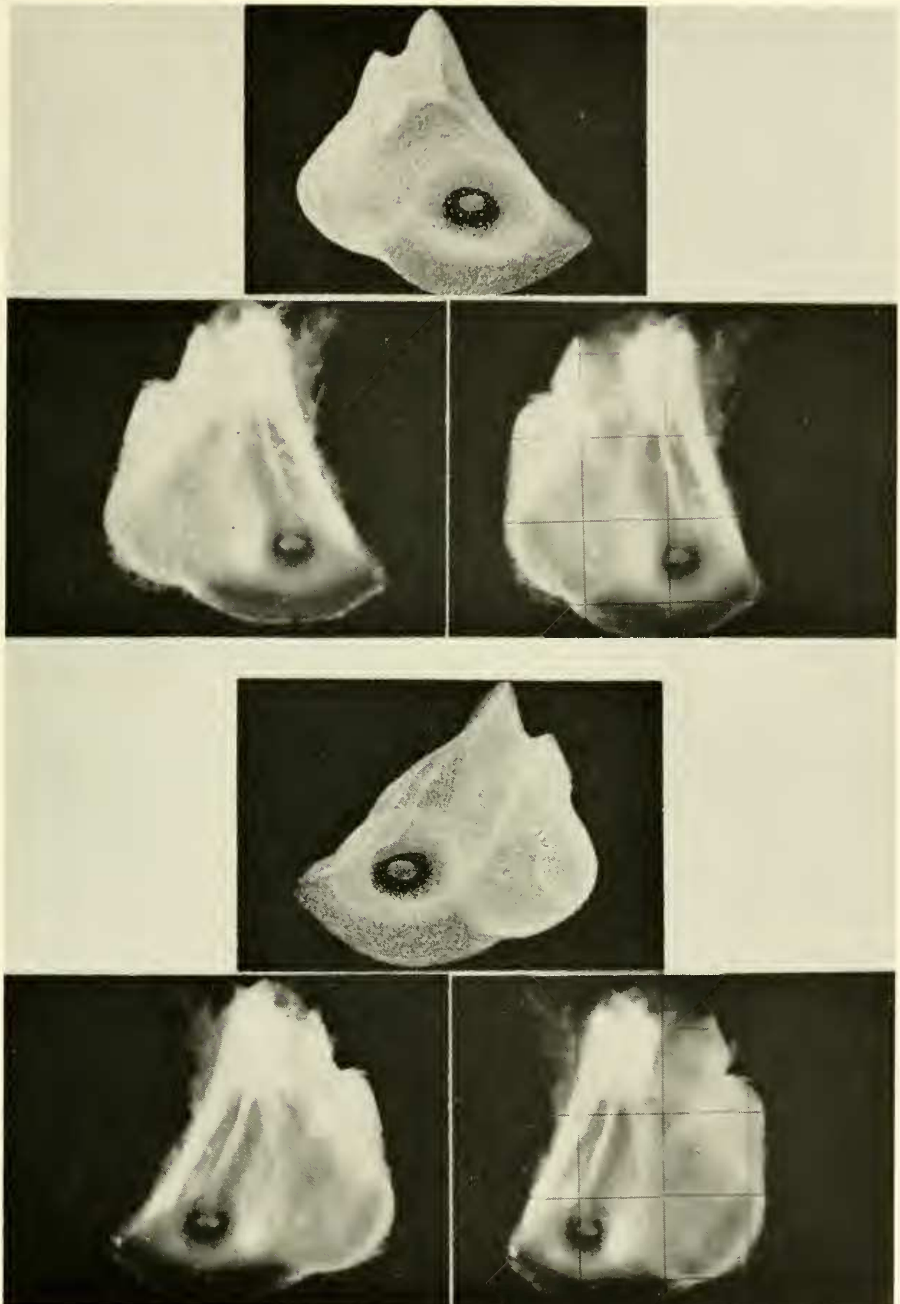

Plate VI. The cochlear duct of *Xenosaurus grandis* (Xenosauridae).

PLATE VII

Family HELODERMATIDAE

Heloderma suspectum (CAS [6])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 14

Stereopair × 18 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The opaque white structure in the upper midportion of the photographs is a portion of the auditory nerve; the branch to the posterior ampulla has been cut off, but the branches to the papilla basilaris and macula lagenae remain.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 14

Stereopair × 18 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The large nerve branch to the papilla basilaris is visible in the upper central portion of the photographs. Note that this nerve branch is bifid just before it enters the basilar membrane. A short superior limbic recess is present.

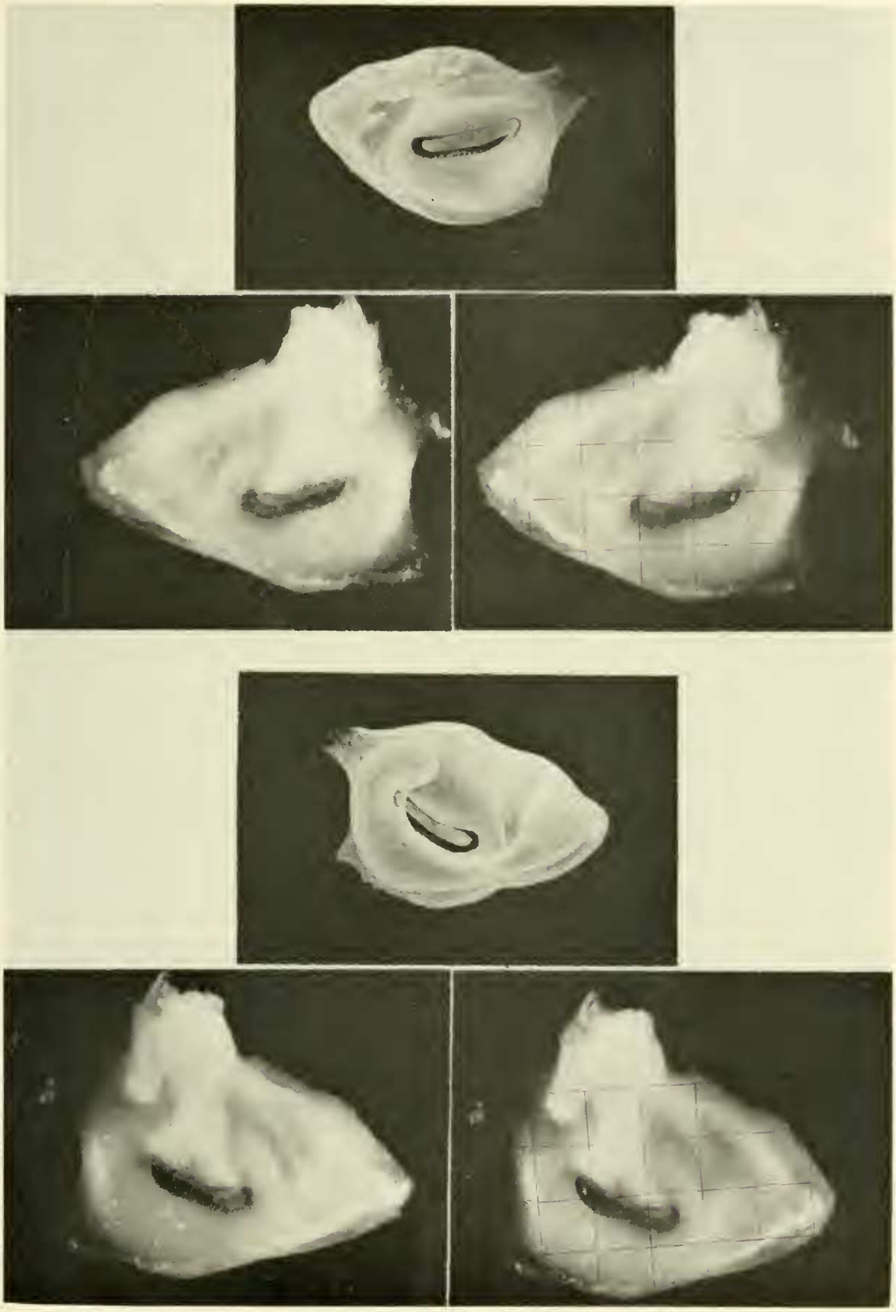

Plate VII. The cochlear duct of *Heloderma suspectum* (Helodermatidae).

PLATE VIII

Family VARANIDAE

Varanus sp. (CAS [24])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 12

Stereopair × 19 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. A divided papilla basilaris is clearly evident in this specimen. In some specimens the papilla is not divided. The neural limbus has no lip, but is thickened. The macula lagenae runs down the anterior (left) edge of the duct and then onto the medial wall of the lagena.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 12

Stereopair × 17 (one grid division = 0.58 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The macula lagenae can be seen running down the anterior wall (right edge) of the duct. A moderately long superior and a short inferior limbic recess are present.

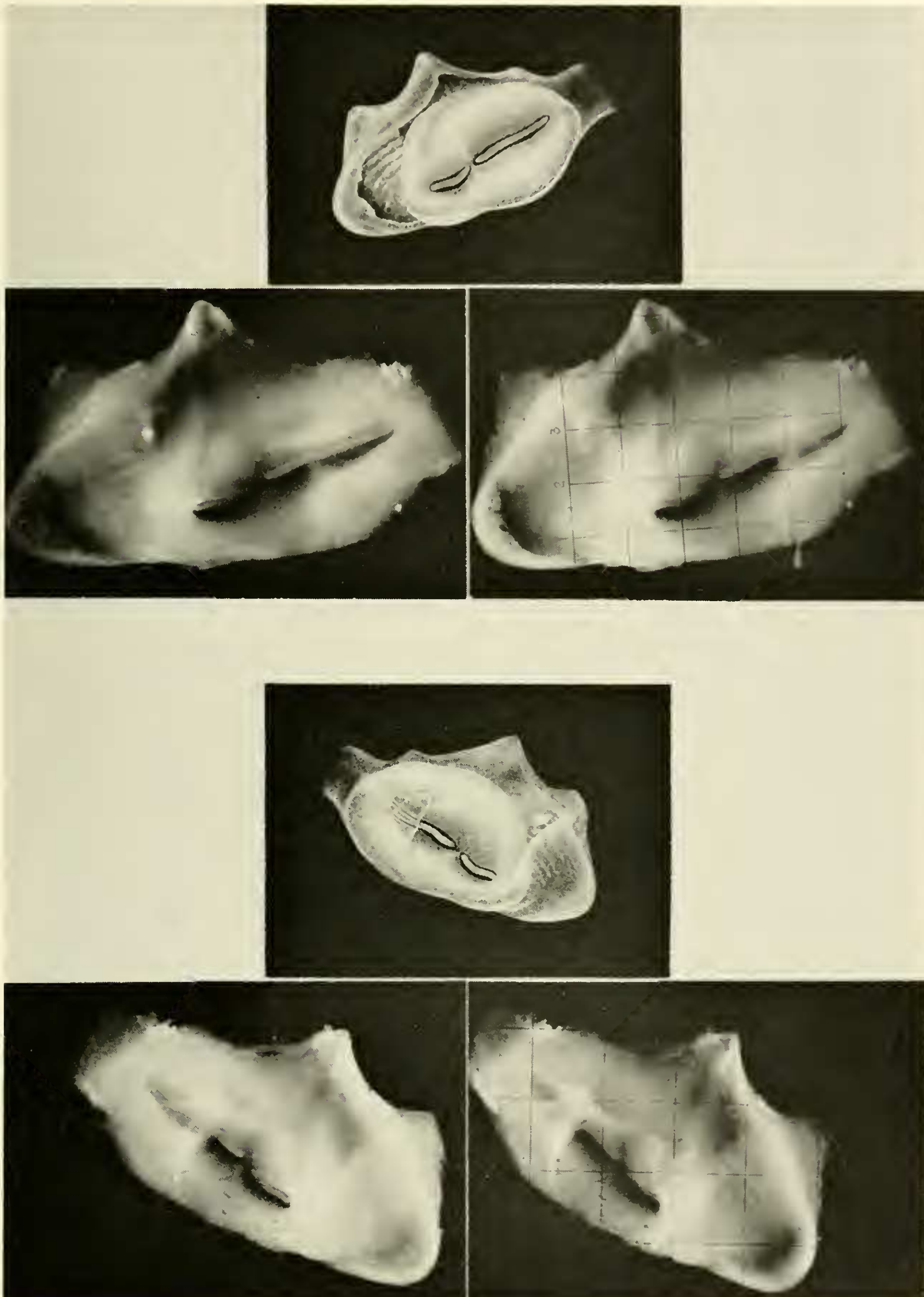

PLATE VIII. The cochlear duct of *Varanus* sp. (Varanidae).

PLATE IX

Family LACERTIDAE

Acanthodactylus cantoris (CAS 86555 [180])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 33

Stereopair × 40 (one grid division = 0.25 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The macula lagenae passes along the inner anterior wall (from right to left, upper edge of the figure) and onto the inferior medial wall of the duct. The nerves supplying the macula lagenae are well shown in the medial view. A well developed limbic lip, and a divided limbic hiatus and papilla basilaris are clearly evident.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 33

Stereopair × 40 (one grid division = 0.25 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The nerves to the macula lagenae and short superior and inferior limbic recesses are evident.

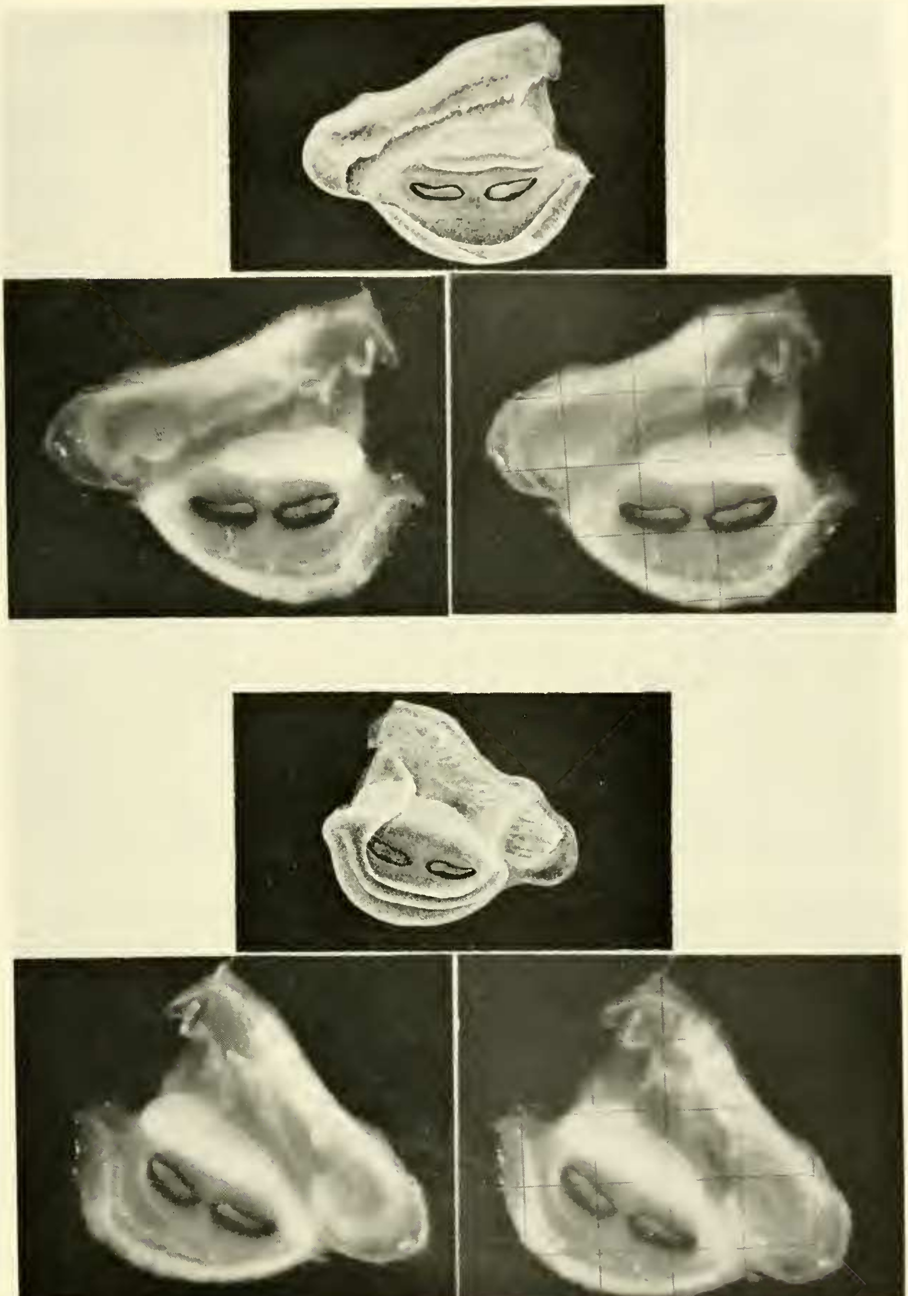

Plate IX. The cochlear duct of *Acanthodactylus cantoris* (Lacertidae).

PLATE X

Family TEIIDAE

Cnemidophorus tigris (CAS 88328 [2])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 18

Stereopair × 26 (one grid division = 0.25 mm.)

Posterosuperior is to the upper right, and anteroinferior to the lower left. The vestibular membrane has been removed. The posterosuperior tip (upper right end) of the limbic lip is broken in the photographed specimen. The macula lagenae runs down the inner aspect of the anterior (left) edge of the duct. Its medial portion is better seen in the medial view below. The calcium carbonate in the otolithic membrane overlying the macula lagenae has been removed with weak acid.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 18

Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the upper left, and anteroinferior to the lower right. The macula lagenae courses along the anterior (right slope) edge of the duct, and then curves onto the inferior medial wall. Short superior and inferior limbic recesses are visible.

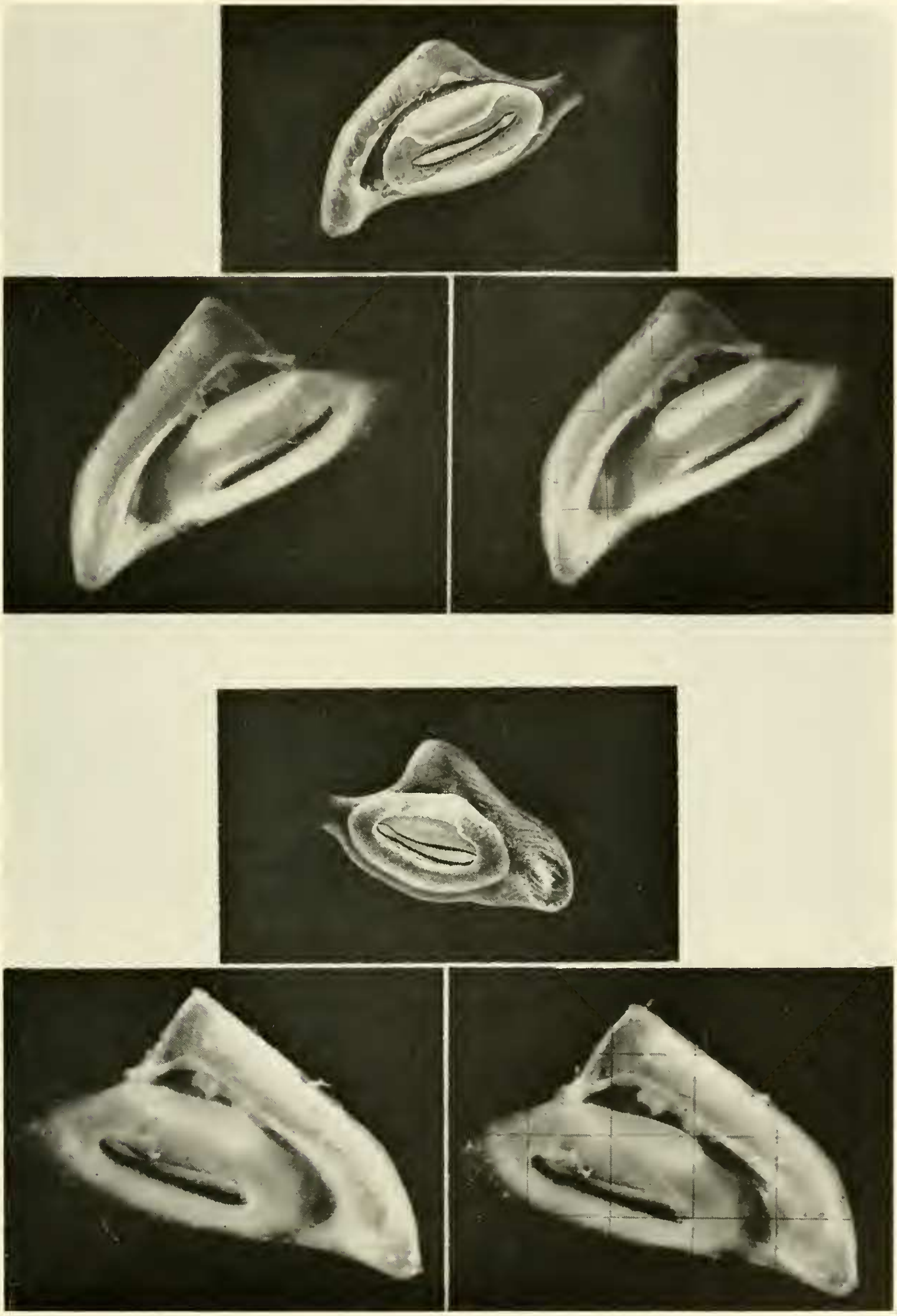

Plate X. The cochlear duct of *Cnemidophorus tigris* (Teiidae).

PLATE XI

Family GEKKONIDAE

Drawing: *Hemidactylus persicus* (CAS 86454 [128])

Photographs: *Cosymbotus platyurus* (SU 18566 [148])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 27

Stereopair × 33 (one grid division = 0.39 mm.)

Posterosuperior is to the upper right, and anteroinferior to the lower left. The vestibular membrane has been removed. The macula lagenae runs down the inner anteroinferior (left) edge of the duct. In the stereophotos, the tectorial membrane extends inferomedially from the tip of the limbic lip over the papilla basilaris (compare with fig. 7).

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 27

Stereopair × 33 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior to the lower right. A relatively long superiorly directed limbic recess is apparent (compare with fig. 6 [insert]).

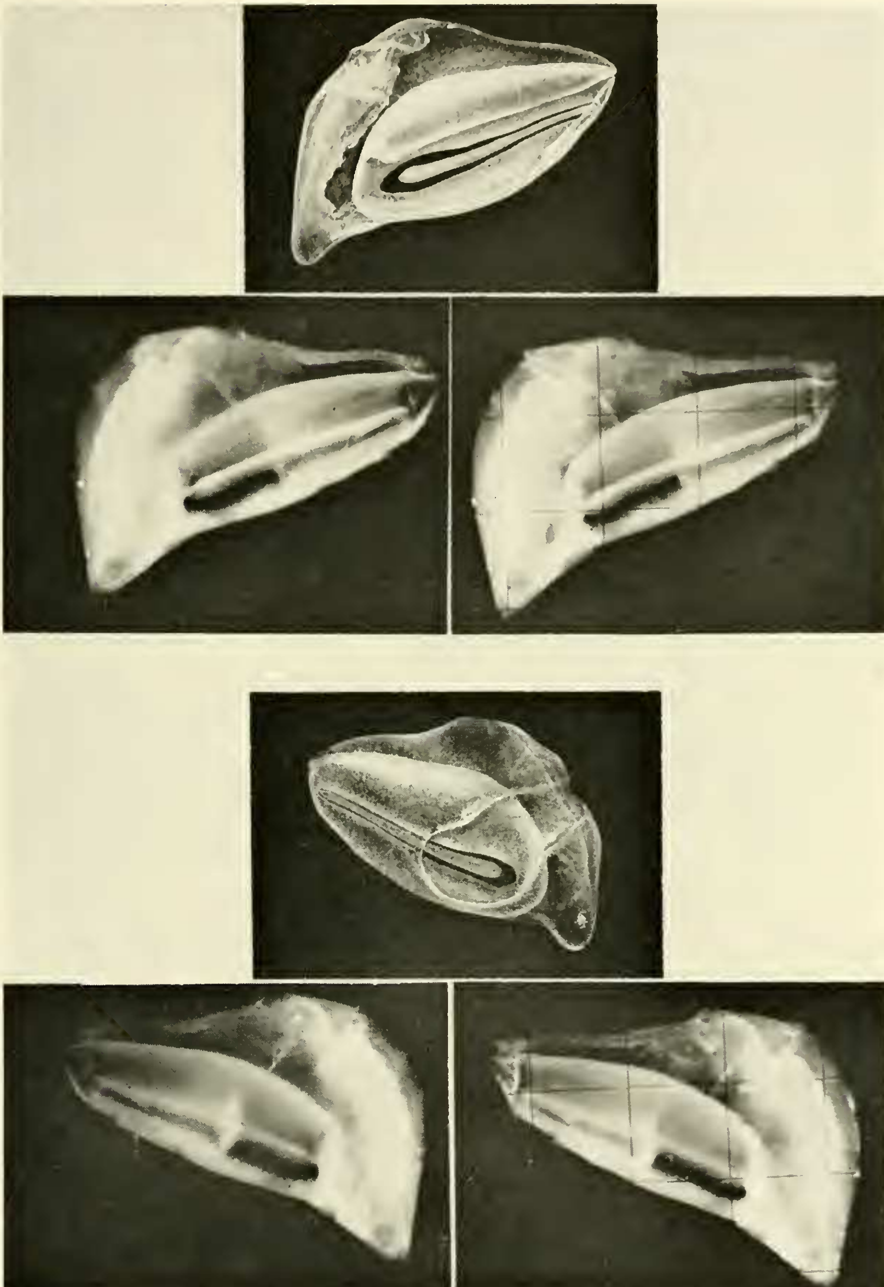

Plate XI. The cochlear duct of *Hemidactylus persicus* (Gekkonidae).

PLATE XII

Family PYGOPODIDAE

Lialis burtonis (CAS 77655 [34])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 18

Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The macula lagenae is a curved band running along the inner anterior edge of the duct. Note that the macula lagenae is nearly parallel to the papilla basilaris. The extensive awning-like limbic lip is clearly apparent.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 18

Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The groove for the perilymphatic duct courses around the anterior (middle top of photographs) edge of the duct and onto its medial surface. Note the long superiorly directed limbic recess.

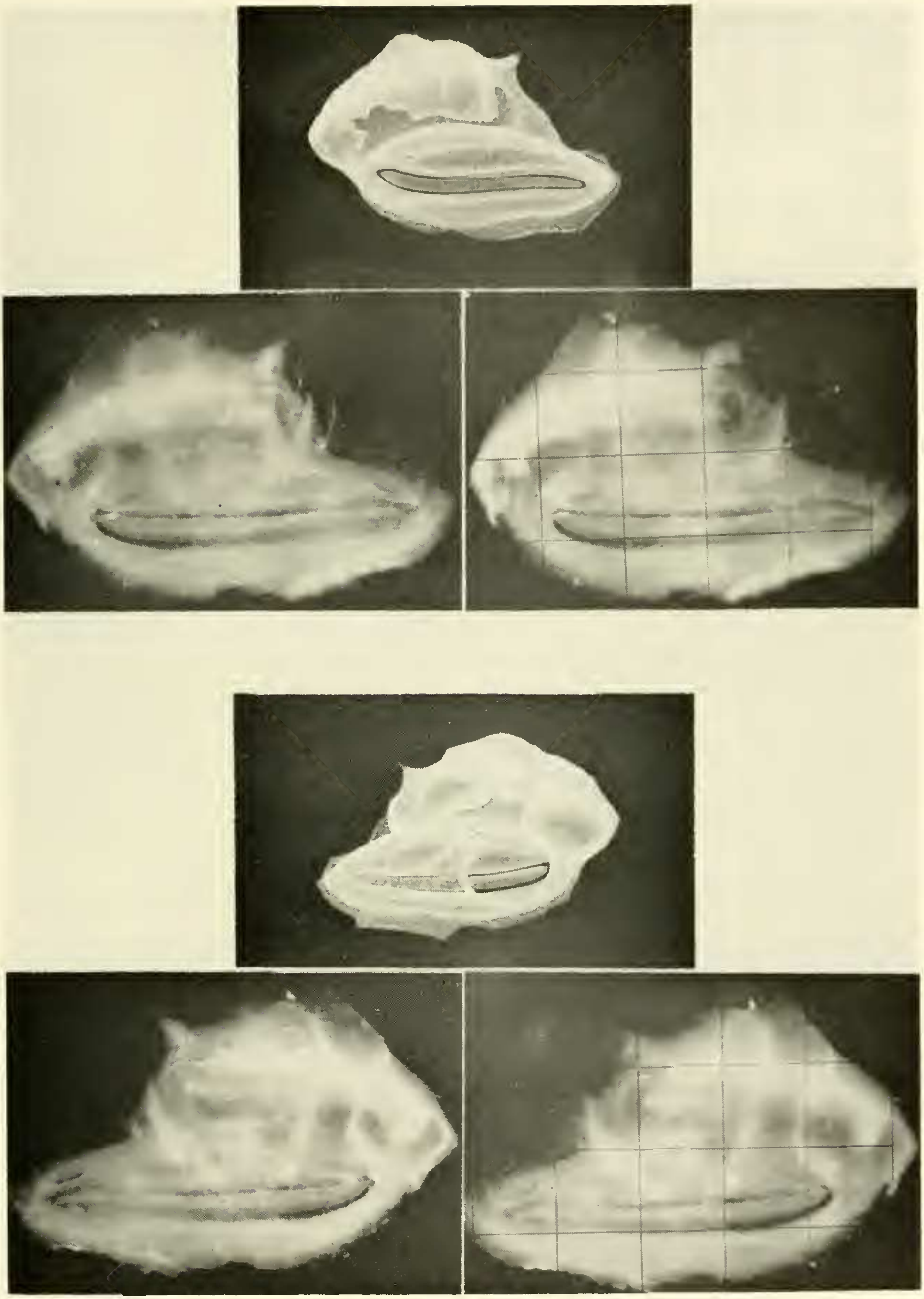

Plate XII. The cochlear duct of *Lialis burtonis* (Pygopodidae).

PLATE XIII

Family SCINCIDAE

Mabuya multicarinata (CAS 60435 [74])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 19

Stereopair × 27 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The macula lagenae is seen coursing from anterosuperior to anteroinferior (upper left) and then onto the inferomedial portion of the duct. The limbus is convex, with the convexity directed laterally (toward the viewer).

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 19

Stereopair × 27 (one grid division = 0.39 mm.)

Posterosuperior is to the upper left, and anteroinferior to the lower right. There is a slight tear between the anteroinferior tips of the pars lagena and the anteroinferior end of the limbus in the stereophotographs. The nerve to the papilla basilaris fans out as it supplies the papilla. The inferiorly directed, relatively long limbic recess is better seen in the drawing. The groove on the midportion of the duct houses the perilymphatic duct.

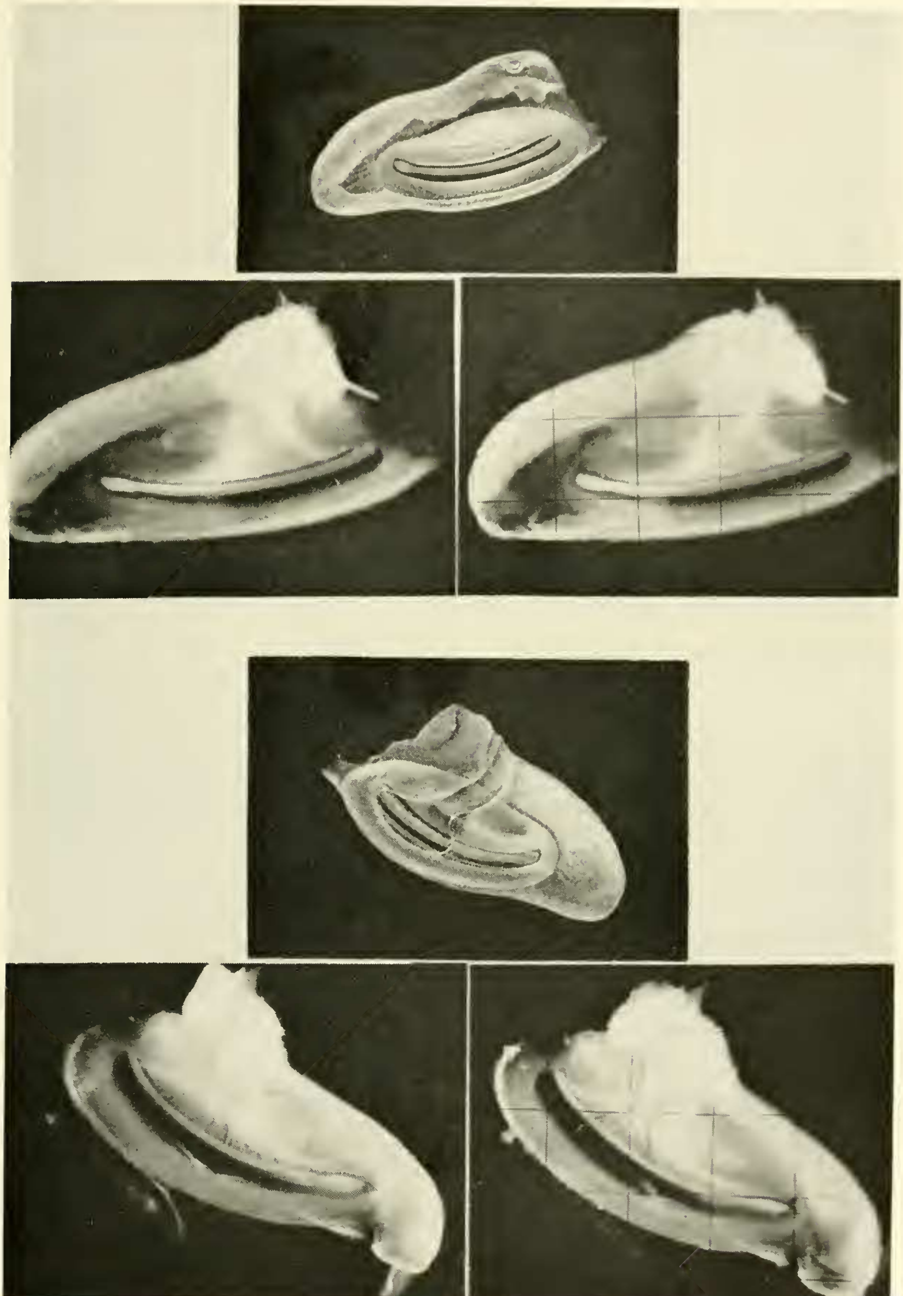

Plate XIII. The cochlear duct of *Mabuya multicarinata* (Scincidae).

PLATE XIV

Family FEYLINIIDAE

Feylinia currori (CAS 55111 [183])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 29

Stereopair × 38 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The anterior (lagenar) edge of the duct has a right-angle bend in its midportion. The greater portion of the macula lagenae occupies the anteroinferior end of the lagenar portion of the duct. A certain amount of precipitated protein and cellular debris obscures the details of the lateral side of the limbus in the photographs.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 29

Stereopair × 38 (one grid divsion = 0.39 mm.)

Posterosuperior is to the lower left, and anteroinferior to the upper right. The perilymphatic duct courses superiorly on the medial face of the cochlear duct. Note the long inferiorly directed limbic recess.

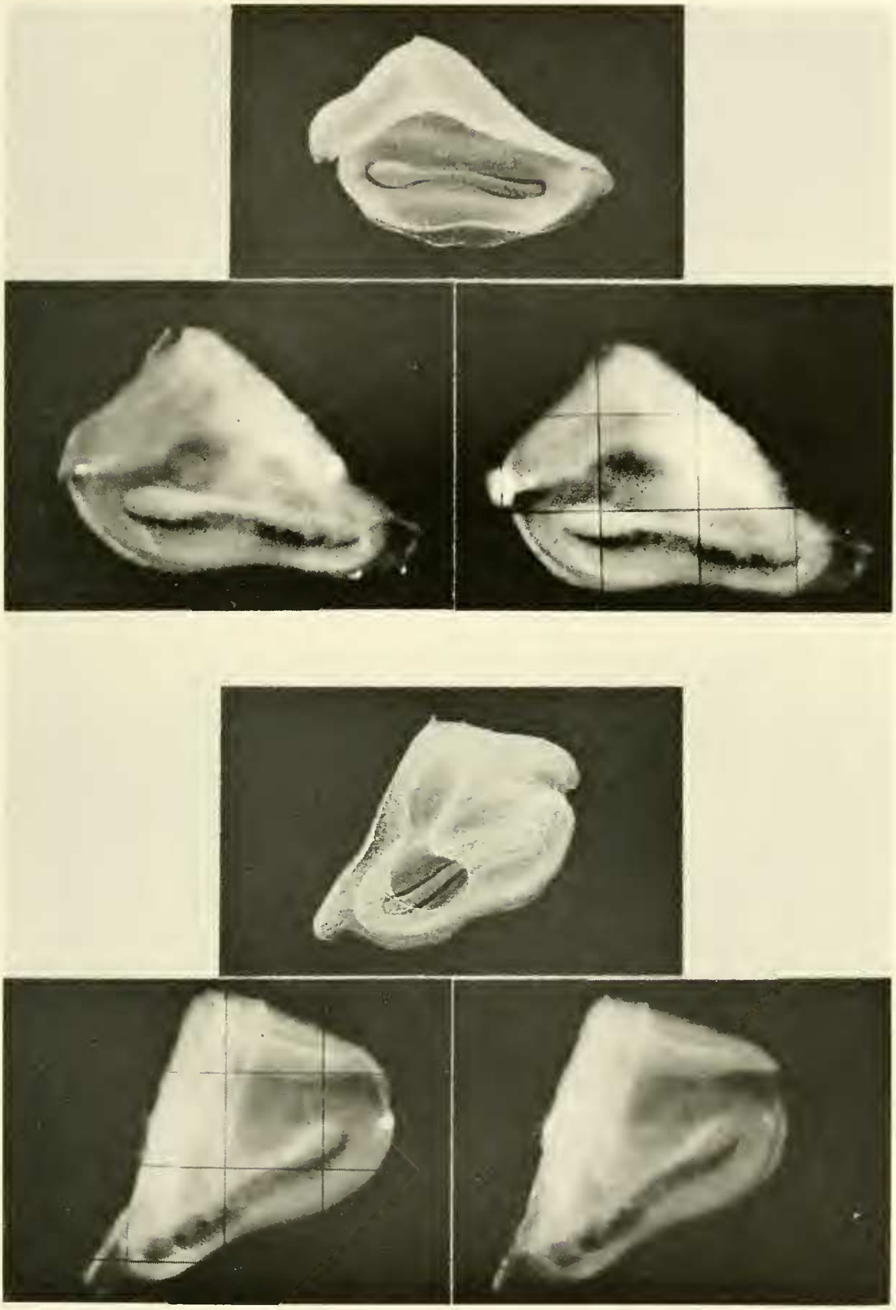

Plate XIV. The cochlear duct of *Feylinia currori* (Feyliniidae).

PLATE XV

Family XANTUSIIDAE

Klauberina riversiana (CAS 43848 [28])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 22

Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the upper right, and anteroinferior to the lower left. The vestibular membrane has been removed. The macula lagenae courses along the inner anterior (left) portion of the duct. The inferiormost portion of the macula lagenae is almost at a right angle to the papilla basilaris. The inferior tip of the papilla basilaris is separated from the superior portion.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 22

Stereopair × 28 (one grid division = 0.39 mm.)

Posterosuperior is to the upper left, and anteroinferior to the lower right. There is a relatively long inferior limbic recess (lower right). In the photograph the nerve to the papilla basilaris spreads out as it supplies the papilla. The nerve to the macula lagenae courses anteroinferiorly (to the right). Comparison of plates 13 and 15 reveals the striking similarities between the xantusiid and scincid cochlear ducts.

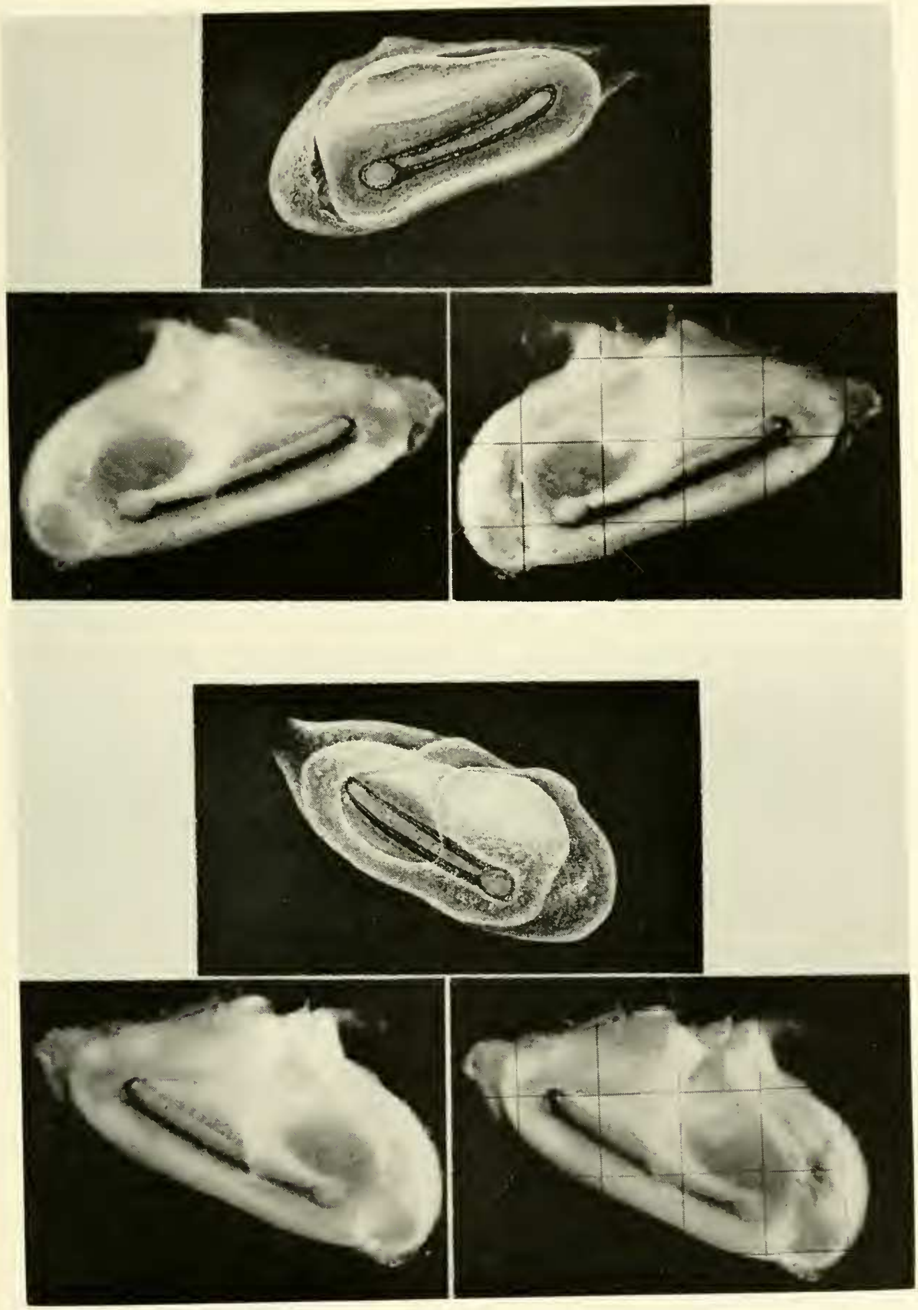

Plate XV. The cochlear duct of *Klauberina riversiana* (Xantusiidae).

PLATE XVI

Family CORDYLIDAE

Cordylus jonesii (CAS [290])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 18

Stereopair × 20 (one grid division = 0.58 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. A portion of the saccular wall is attached to the cochlear duct in the photographs. The macula lagenae courses down the anteroinferior edge of the duct. The nerve to the papilla basilaris fans out to supply the papilla.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 16

Stereopair × 20 (one grid division = 0.58 mm.)

Posterosuperior is to the upper left, and anteroinferior points downward. The nerve to the posterior ampulla has been cut off while the nerves to the papilla basilaris and macula lagenae are present in the photographs. Short superior and inferior limbic recesses are best demonstrated in the drawing.

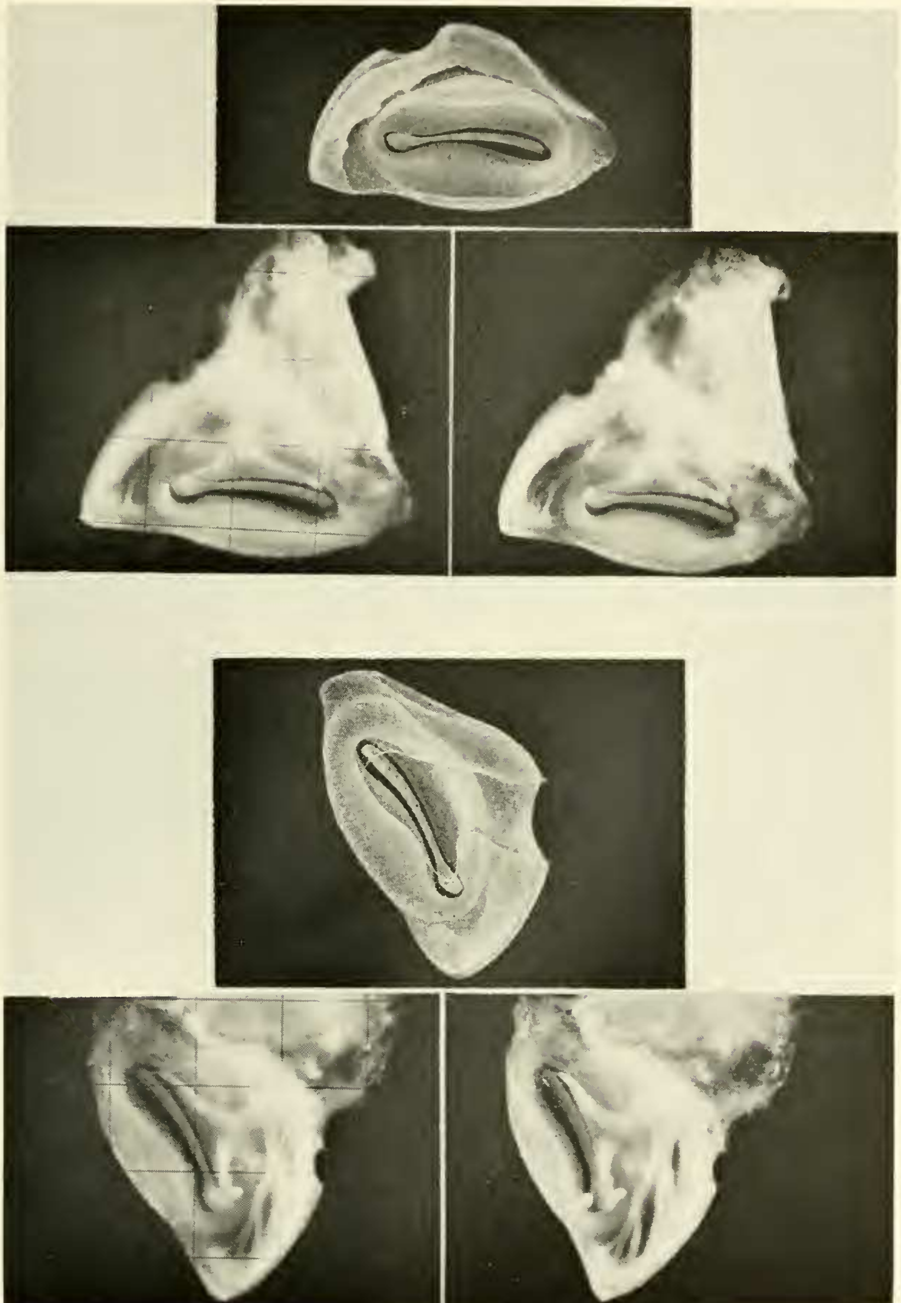

Plate XVI. The cochlear duct of *Cordylus jonesii* (Cordylidae).

PLATE XVII

Family DIBAMIDAE

Dibamus argenteus (SU 18761 [341])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 39

Stereopair × 33 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed in the drawing, but is intact in the photographs. A portion of the posterior semicircular canal and the posterior ampulla is present in the photographs. The inferior wall of the sacculus seems to be fused to the anterosuperior wall of the cochlear duct. A larger portion of the saccular wall is shown in the photograph. The small lagena forms the left (anteroinferior) end of the duct.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 39

Stereopair × 33 (one grid division = 0.39 mm.)

Posterosuperior is to the left, and anteroinferior to the right. Note the groove for the perilymphatic duct on the medial face of the duct and the nerve branch supplying the papilla basilaris in the photographs.

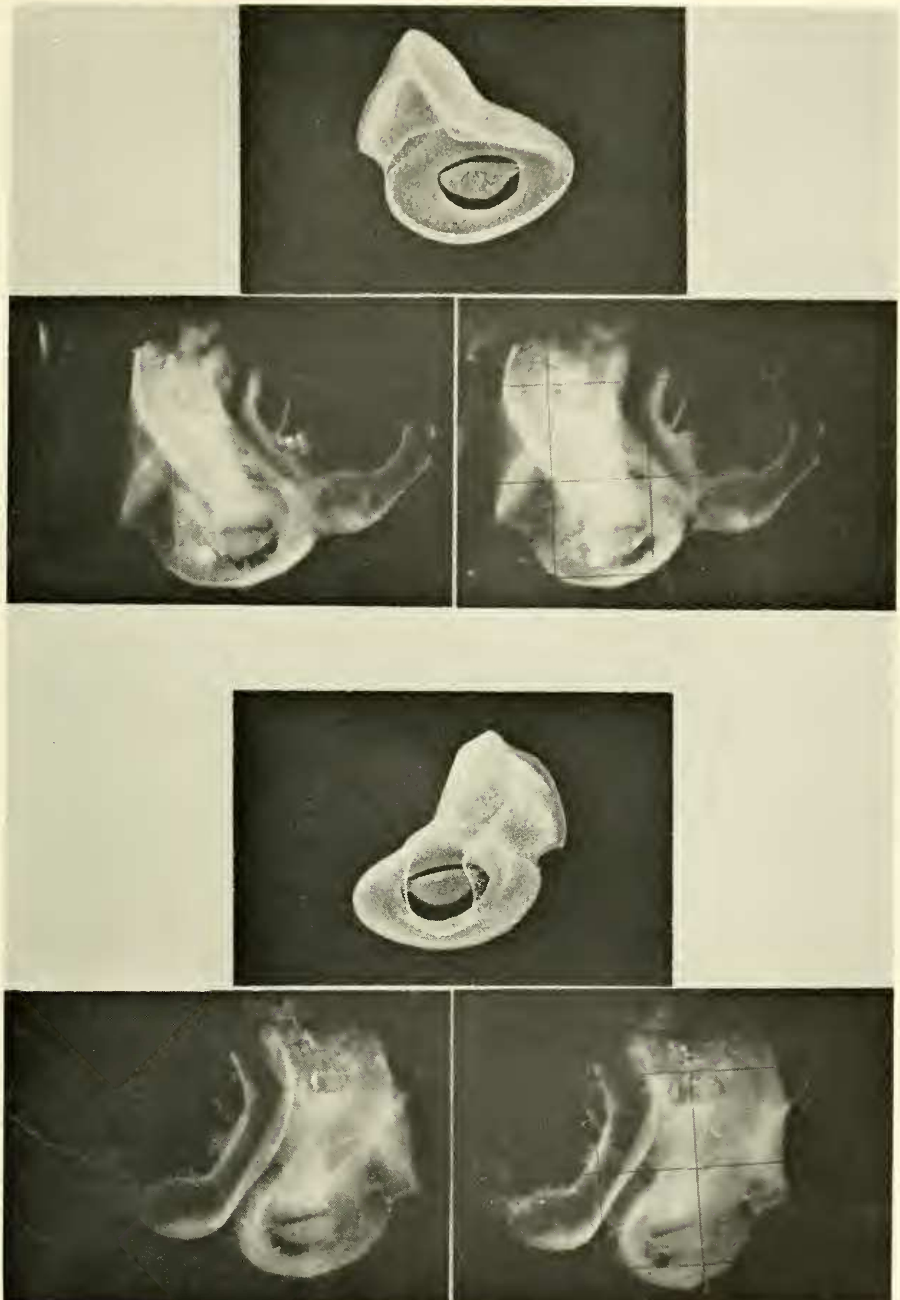

Plate XVII. The cochlear duct of *Dibamus argenteus* (Dibamidae).

PLATE XVIII

Family AMPHISBAENIDAE

Amphisbaena fuliginosa (CAS 71336 [227])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 22

Stereopair × 29 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane is intact. The macula lagenae lying on the left (anteroinferior) end of the duct is covered by an opaque white otolithic membrane. In most other specimens the calcium carbonate which was present in the otolithic membrane was dissolved away with weak acid, as it usually obscures the general structure. The limbic lip lies at the upper (anterior) edge of the neural limbus.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 29

Stereopair × 36 (one grid division = 0.39 mm.)

Posterosuperior is to the left, anteroinferior to the right. The white elongate structure on the right-hand side of the photograph is the nerve to the macula lagenae. The perilymphatic groove and part of the medial portion of the basilar membrane is obscured by a membrane in the photograph.

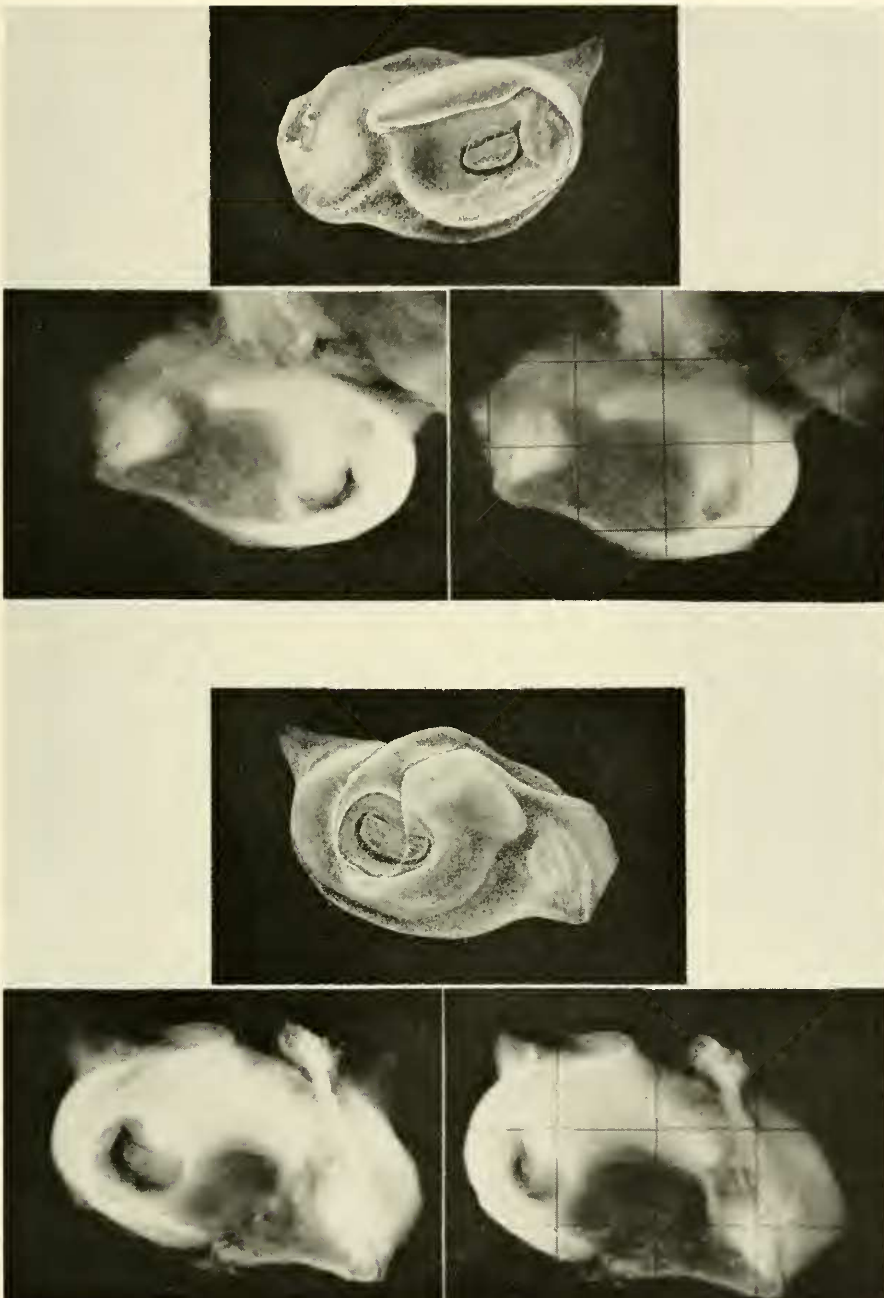

Plate XVIII. The cochlear duct of *Amphisbaena fuliginosa* (Amphisbaenidae).

PLATE XIX

ORDER OPHIDIA

Family COLUBRIDAE

Pituophis catenifer (CAS [291])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 22

Stereopair × 29 (one grid division = 0.39 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The large lagenar sac lies to the left and the smaller limbic portion of the duct to the right. The apparent shelflike projection above the neural limbus seems to be an area of fusion between the sacculus and the anterior edge of the neural limbus. In the photograph, the distal, broken end of the nerve to the papilla basilaris is seen. The outlines of the perilymphatic duct sweeping from the lateral surface of the duct around to the medial aspect of the basilar membrane are evident in both lateral and medial views. The macula lagenae is an opaque white band on the anterior and medial inner surfaces of the lagenar sac.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 22

Stereopair × 29 (one grid division = 0.39 mm.)

Posterosuperior is to the upper left, and anteroinferior to the lower right. The course of the perilymphatic duct sweeps from the right upper side of the photo over to the medial aspect of the papilla basilaris. The nerves to the macula lagenae supply the band-like macula lagenae.

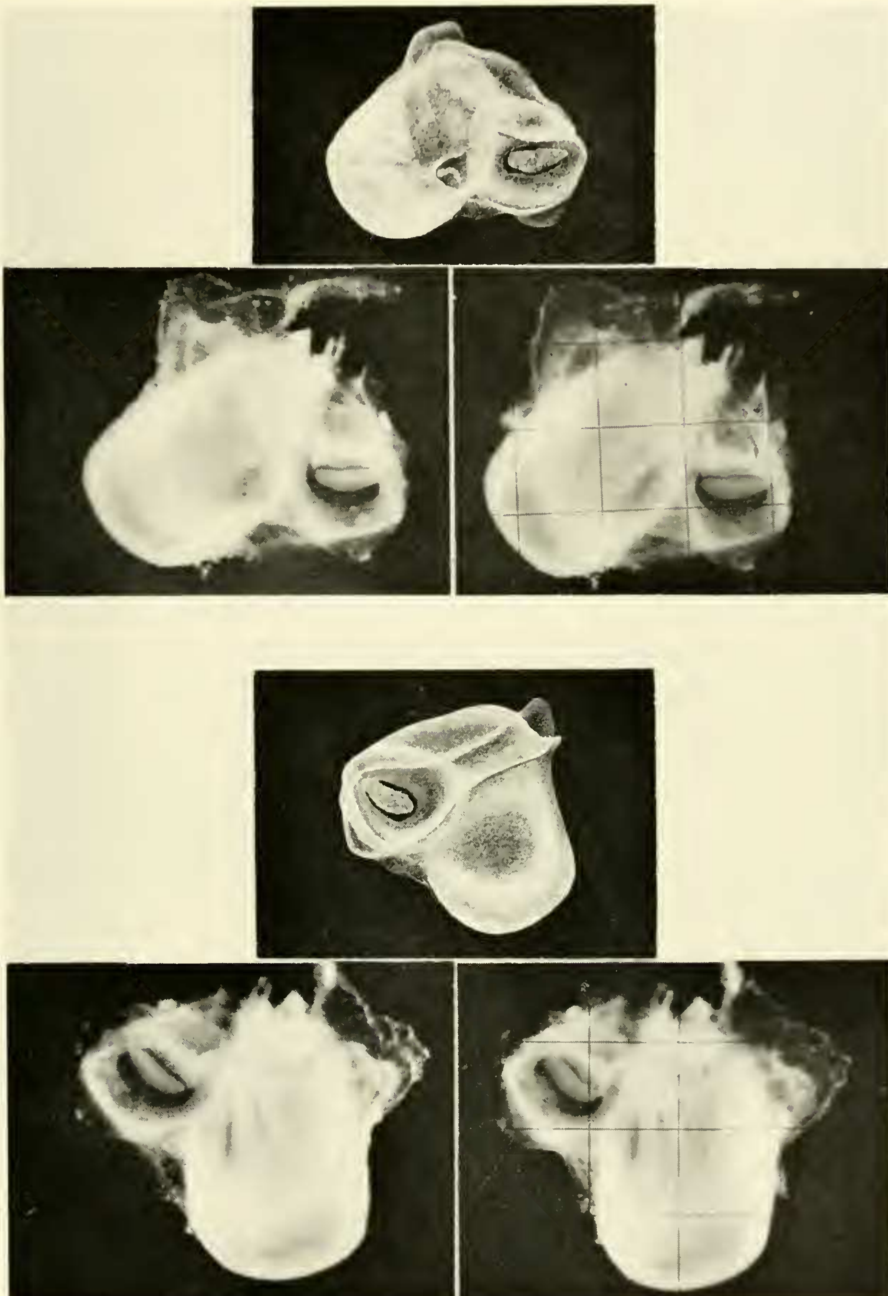

Plate XIX. The cochlear duct of *Pituophis catenifer* (Colubridae).

PLATE XX
SUBORDER CHELONIA
Family TESTUDINIDAE
Gopherus berlandieri (CAS [46])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 12
Stereopair × 12 (one grid division = 0.58 mm.)

Posterosuperior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The inferior wall of the sacculus (sac-like structure situated above in the drawing) remains attached (it seems to be fused) to the anterosuperior wall of the cochlear duct. The solid white structure running posterior (downward) in the photograph is the nerve to the crista of the posterior semicircular canal. The fuzzy processes surrounding the cochlear duct are trabecular connective tissue strands that attach the cochlear duct to the periosteum of the otic capsule. The ovate papilla basilaris is seen in the lower midportion of the pictures.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 12
Stereopair × 12 (one grid division = 0.58 mm.)

Posterosuperior is above, and anteroinferior below. The structure projecting to the left in the photograph is the nerve to the posterior crista. The nerves to the papilla basilaris and macula lagenae are also quite obvious in the photograph. The cavity in the midportion of the photograph is the groove for the perilymphatic duct as it sweeps around from the lateral to the medial surface (right side of the photograph) of the duct and then becomes the scala tympani portion of the perilymphatic sac where it lies over the basilar membrane.

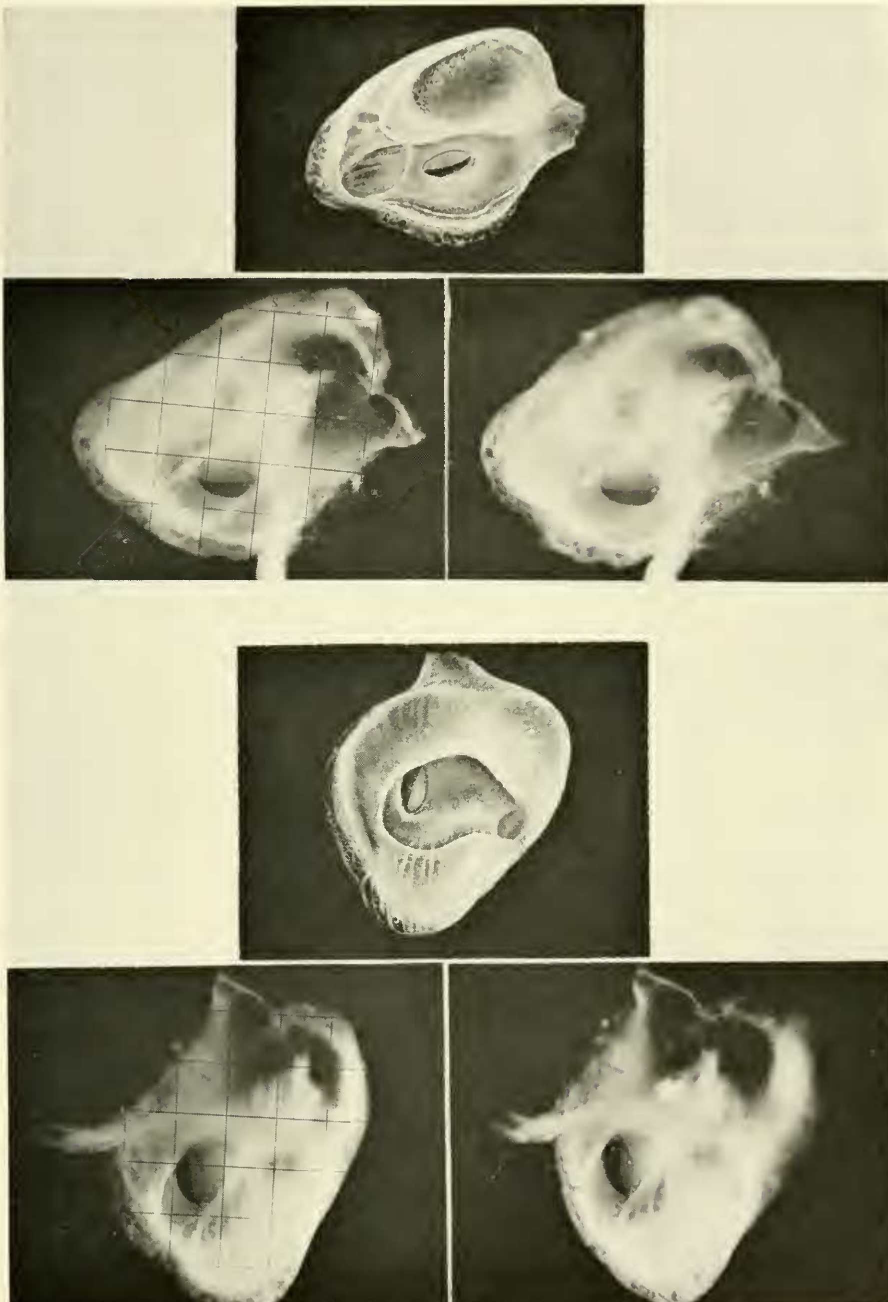

Plate XX. The cochlear duct of *Gopherus berlandieri* (Testudinidae).

PLATE XXI

ORDER RHYNCHOCEPHALIA

Family SPHENODONTIDAE

Sphenodon punctatum (CAS [40])

Upper Group: Drawing and stereophotographic pair of the lateral aspect of the left cochlear duct.

Drawing × 9
Stereopair × 13 (one grid division = 0.76 mm.)

Posteroinferior is to the right, and anteroinferior to the left. The vestibular membrane has been removed. The sac-like pars lagena lies to the left and the limbic portion to the right. The basilar membrane is stretched across the lateral end of a tubelike limbus. The papilla basilaris has not been well preserved, but the residual outlines may be made out. The macula lagenae sweeps around the midportion of the lagena as a band-like area running from the lateral to the anterior and then onto the medial aspect. This is better seen in the medial view. Debris from the otolithic membrane lies within the lagenar sac.

Lower Group: Drawing and stereophotographic pair of the medial aspect of the left cochlear duct.

Drawing × 9
Stereopair × 13 (one grid division = 0.76 mm.)

Posterosuperior is to the left, and anteroinferior to the right. The medial side of the limbus appears as a tubelike or deeply excavated pocket with the basilar membrane stretched across its lateral end. Two triangular arm-like processes almost close over a portion of the back of the limbus. The perilymphatic duct opens into the scala tympani portion of the perilymphatic sac above (anteromedial) these two arms and the large medial opening is the site of connection of the scala tympani with the perilymphatic sac proper.

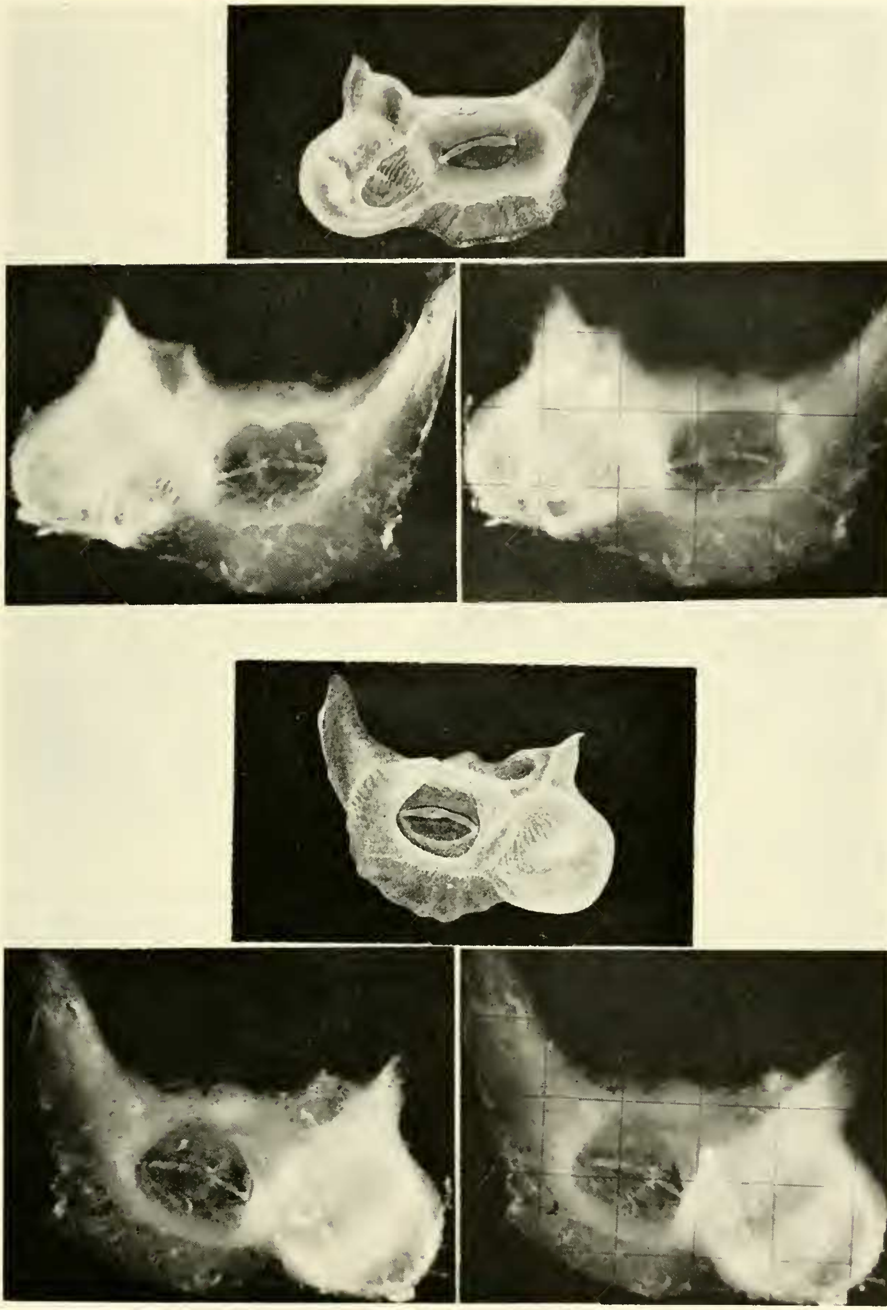

PLATE XXI. The cochlear duct of *Sphenodon punctatum* (Sphenodontidae).

PLATE XXII

Summary plate comparing the lateral aspect of the cochlear duct in lizard families

Drawings of the lateral view of the left cochlear ducts from representatives of different families of lizards and an example of a snake, a turtle, and *Sphenodon*.

The cochlear ducts are not drawn to the same scale.

The cochlear ducts are arranged according to my present concept of the possible relationships between different lizard families as determined in part by the anatomical similarities in cochlear duct anatomy (see Discussion for further details).

I.	Iguanidae	Agamidae	III.	a. Anguidae	b. Anniellidae
II.	Chamaeleonidae			c. Xenosauridae	d. Helodermatidae
V.	Lacertidae	Teiidae	IV.	Varanidae	
VI.	Gekkonidae	Pygopodidae	VIII.	Dibamidae	IX. Amphisbaenidae
VII.	a. Scincidae	b. Feyliniidae	Snake—Colubridae		Turtle–Testudinidae
	c. Xantusiidae	d. Cordylidae		*Sphenodon*	

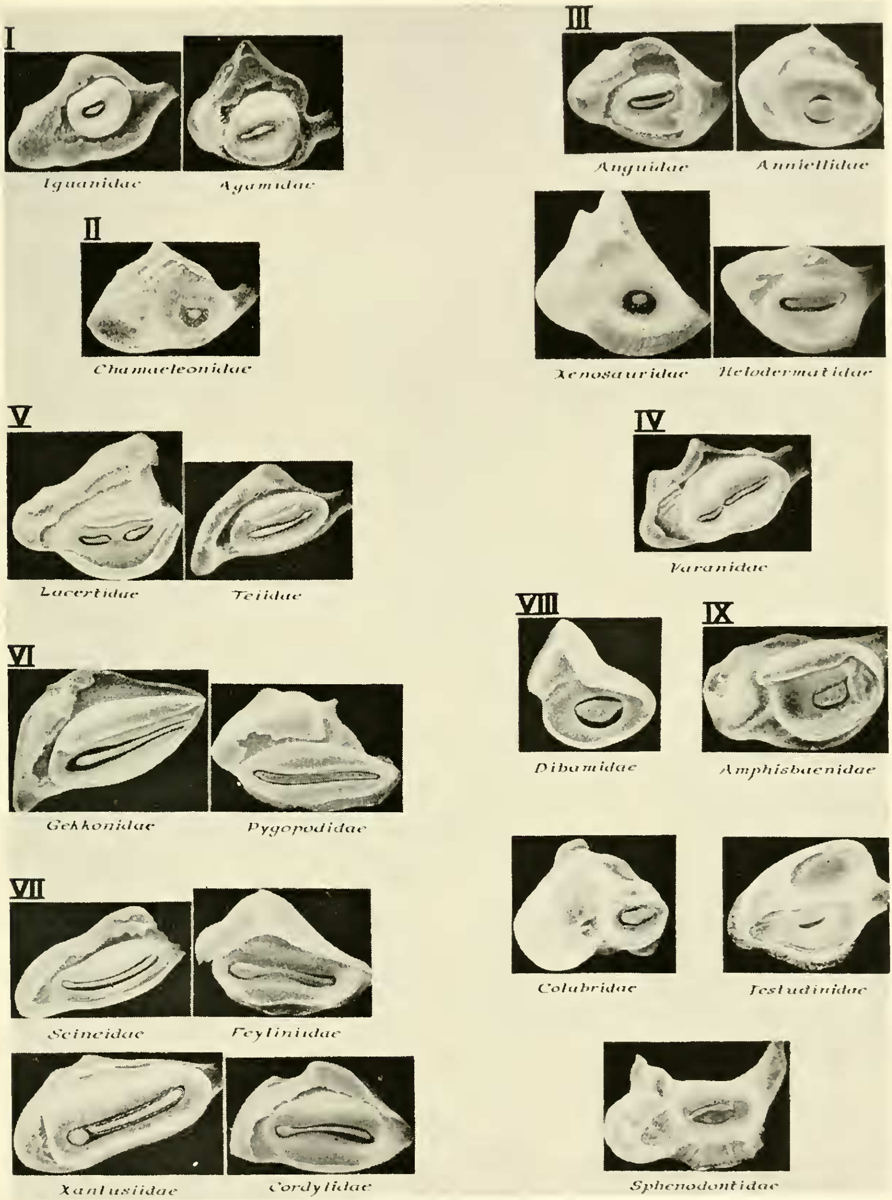

PLATE XXII. Summary plate comparing the lateral aspect of the cochlear duct in lizard families.

PLATE XXIII

Summary plate comparing the medial aspect of the cochlear duct in lizard families

Drawings of the medial view of the left cochlear ducts from representatives of different families of lizards and an example of a snake, a turtle, and *Sphenodon*.

The cochlear ducts are not drawn to the same scale.

For explanation of arrangement see plate XXII.

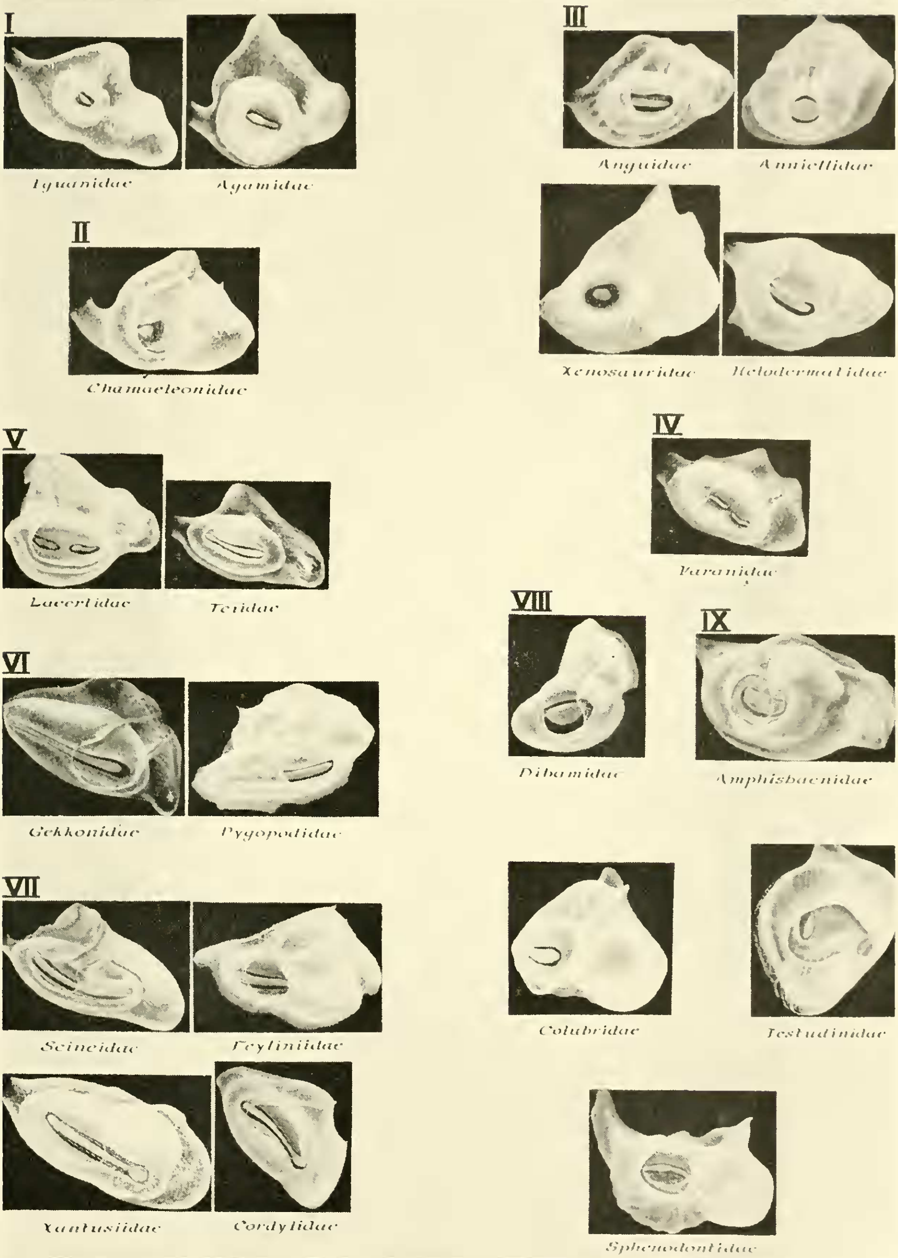

Plate XXIII. Summary plate comparing the medial aspect of the cochlear duct in lizard families.